THE SOCIAL WORLD OF THE ANTS

AUGUSTE FOREL.

Frontispiece Vol. I.

THE SOCIAL WORLD OF THE ANTS

COMPARED WITH THAT OF MAN

BY

AUGUSTE FOREL

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TRANSLATOR'S FOREWORD

There are scientists who hold that in due course Man will yield to the Ant the mastery of a planet grown less hospitable to the relatively idle and unorganized. Certainly man's curiosity as to his potential executors has been increasing of late, and Forel's *magnum opus* reaches the English-speaking public at an opportune moment.

For the last few years entomologists have made constant contributions to the most significant biological issues. Not only the major problems of Sex in all its gradations, and of Symbiosis in relation to parasitology and disease, but the habitability of the tropics and even the future of our food supply are now their intimate concern. We are learning to respect the ants both as weavers, with their use of tools, and as architects, with their elaborate masonry; to observe with more understanding their games, their wars, their cattle-breeding, their hygiene, their eyeless sight, and their powers of orientation. Statisticians concerned with the population problem, no less than philosophers involved in controversies raised by the phrase Emergent Evolution, are now going to the ants; and as humanity becomes more disturbed about the aims and implications of specialization, the sociologist, too, will elaborate on page 290 of Volume II.

Moreover, there is their language. When, in 1918, the Orthological Institute was founded, for the systematic study of the influence of Language on Thought, the problem of animal communication was naturally in the forefront in its programme. With the subsequent widening of the scientific field to include all forms of symbolism and interpretation—signs, codes, and notations—the ant became hardly less important than the chimpanzee for those in search of new light on old mysteries. If, therefore, the reader will turn to page 240 or 447 of Volume I, he will see the reason why some psychologists feel that they cannot learn too much about creatures whose technique is in so many respects more highly developed than our own.

My first debt as translator is to the author himself, with whom I have been continuously in touch since the publication of a résumé of these volumes, through the good offices of Professor Bronislaw Malinowksi, in *Psyche* (April, 1924). It is now thirty years since Professor Forel retired from active work as Professor of Psychiatry in Zurich to complete his entomological researches; and the thought that the English translation would be in his hands on his 80th birthday has spurred many of his admirers to co-operate in rendering it as adequate a record of his life's work as possible. The publishers, in particular, deserve well of the ant world for the trouble they have taken to make smooth the way of a translator who has seldom been in the country, or even the hemisphere, most convenient for his printers.

Next, I have to thank Professor Edouard Bugnion for permission to use as an Appendix the essay which originally appeared with Part III of the French version. Not only did he very kindly revise the text as late as the summer of 1927, but he has allowed us to use the sketches which appear at pages 277-8 of Volume II (figs. 128, 129, 130), to illustrate the account of weaving ants in his brother-in-law's text.

To Miss E. G. Mountford, Mr. M. R. Dobie, and Mr. Reginald Pott, I am indebted for invaluable assistance at various stages of my labours; to Mr. Cecil Warburton and Professor Balfour Browne I referred sundry difficulties requiring expert advice. I have also been able to consult in person the three authorities whose work will be found most useful to those in search of correlative and supplementary material. Mr. Horace Donisthorpe, whose *British Ants*, already in its second edition, and *Guests of British Ants*, provide the detailed knowledge essential to any investigator in the British Isles, responded to queries with unfailing courtesy. Dr. J. G. Myers, whose *Psychology of Insects* will be added in the fullness of time to the International Library of Psychology, cast a practised eye over the proofs on his return from Australia. And, finally, it was my privilege 'while in America in 1926, and again in 1927, to enjoy the hospitality of that master of modern scientific entomology, Professor William Morton Wheeler, of Harvard.

Professors Wheeler's *Insect Societies*, following his *Emergent Evolution and the Social* in the *Psyche* Miniatures, is shortly to join Alverdes' *Social Life in the Animal World* in the section of the International Library devoted to Animal Sociology. His excellent Bibliography and copious references to the literature of the past ten years have made it unnecessary to burden Forel's pages with critical and supplementary material.[1] Those for whom such material

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[1] While these pages were passing through the press, Forel himself read Wheeler's edition of Réaumur's *Natural History of Ants* (1926), and noted various observations for which Réaumur must be given priority.

As regards a few minutiæ in the text, the English student may also be glad to have the following references:—Donisthorpe holds that Wasmann's theory of *Atemeles* and pseudogynes (Vol. I, p. 276), as cause and effect, has now been definitely disproved, claims to have discovered the food of *Microdon* (I, 296), would not regard *Clythra* as an ectoparasite, has found eighteen species of "cattle" in the nests of *flavus* (I, p. 493) in Britain, maintains that *Myrmecina graminicola* (II, p. 58) is far from pacific, has seen coccids with *Ponera coarctata* (II, p. 299) in England, and agrees with Wheeler in making *Pseudomyrmini* a sub-family. Those who have further been apprised that full particulars of British fossil ants (I, 173) can be found in *Ann. Mag. Nat. Hist.*, 1920, that Crawley (1920) has brought the list of Gynandromorphs (I, 325) up to 43, and that Chapman's work on *Lycaena alcon* (1918) supplements the literature cited at Vol. I, p. 508, may regard themselves as in possesssion of the very latest word in scientific myrmecology at home and abroad.

would be appropriate must, in any case, have access to Wheeler's work, while Forel, in summing up a century of entomological research, may remain a classic in the sense that *The Origin of Species* will probably not be out of print for its centenary.

As Professor Wheeler himself writes to me, these two volumes "are extremely important, not only because they are Forel's last great contribution to myrmecology, but because they reveal so much of his wonderful personality." If the reader can approach the work in that spirit, he will neither resent the occasional intrusion of the author's political enthusiasms nor faint by the way because certain passages may at first seem heavy going. In other words, he will refrain from judging it solely in terms of modern popular or scientific book-making.

In conclusion, I cannot do better than quote (with Professor Wheeler's permission), the following further tribute from the same letter:—

> "*Forel is the latest link in a remarkable chain of Swiss naturalists and savants, beginning with Charles Bonnet, who received his inspiration from no less a naturalist than Réaumur, and including François and Pierre Huber, two generations of Agassiz and four generations of Decandolles; and Saussures, Forel is inferior to none of these in his philosophical grasp of biological problems and his contributions to our knowledge of biological facts. His training as a physician, neurologist and psychiatrist, proved to be just the preparation that was needed for his epoch-making elucidation of the sensory and instinctive behaviour of the insects which occupied the centre of his interest even during his early childhood. But his preparation acquired even greater significance because of his sympathetic and inspiring personality, which impelled him to take an effective interest in everything*

that promised moral and social improvement of his fellow men. That a man of such intellectual and moral eminence and so much like Socrates in his solicitude for sane thinking and conduct in himself and others, should have been blessed with so little of this world's goods and comforts, is indeed a sad commentary on our modern pleasure-mad civilization."

January, 1928. C.K.O.

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EXPLANATION OF CERTAIN SPECIAL TERMS FREQUENTLY USED IN THIS WORK

♂—Male.

♀—Female.

☿—Worker.

♃—Soldier.

Apterous—Without wings.

Chromatin—A substance in the cell nucleus, in which chemical reagents produce different colours for the part which comes from the male (the father), and the part which comes from the female (the mother).

Endosmosis—The passage of nutriment through a fine skin or wall, which can be penetrated.

Ergatogyne—Female without wings, analogous to the worker.

Ergatomorphism—The occurrence of forms analogous to that of the worker.

Granivorous—Grain-eating.

Mimetic—That which imitates.

Mimicry—Imitation of form, colour, movement, etc.

Myrmecology—The science of ants.

Myrmex—Greek word, signifying "ant."

Ontogenesis (*Ontogeny*)—Origin and transformation of the *individual* from its egg-stage to its adult stage and even its old age.

Ontogenetic—That which is concerned with ontogenesis.

Oviduct—Canal through which eggs pass out of the ovary and are laid.

Parthenogenesis—Origin of an *individual* from a female only, without the participation of the male.

Phylogenesis (*Phylogeny*)—Origin and successive transformation of *species* from geological times to the present day.

Pleometrosis—Peculiarity of ant-colonies which each contain several fertilized females or queens.

Polymorphism—Constant differences in size, form, aptitude, etc., in certain individuals of the same species.

Protoplasm—Substance of the animal or vegetable cell, generally excluding that of its nucleus.

Pseudogyne—An individual ant which is malformed owing to the action of certain guests or parasites.

Spermatozoon—Special male cell which fertilizes the egg by penetrating it; the equivalent of the female nucleus, which is itself a cell.

Suture—Deep line of demarcation.

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[1] Coloured plates.

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[1] Coloured plates.

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[1] Coloured plates.

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PART II

PART III

PART I.

PREFACE

Friend reader, in presenting you with my last work after seventy-eight years of life, I owe you a few confidences.

I was born on September 1st, 1848. My father was Swiss and my mother came from the South of France. I passed my early childhood, until the age of eight and a half, in the little village of Lonay, near Morges, on the shores of Lake Geneva. Fearing that the unruly urchins of Lonay would have an ill effect upon me, my mother kept me in our garden, which had a terrace with three steps; and between these there lived the inhabitants of an ant-colony. I used to amuse myself by observing them, while my mother was playing Beethoven's sonatas on the piano. Thus it was that from the age of five, ants, wasps, snails, little creatures in general and ants in particular, were my delight. There were big ants, little ants, black, red and yellow ants. And then, inside their nests, which I overturned, there were little white worms and motionless white cocoons looking as if they were swaddling clothes. I watched the nimble ants bearing all these curious things with jealous care; but neither my mother nor I could tell what it all meant. These white objects could not possibly be eggs, because they were often as big as the ants themselves, occasionally bigger. Sometimes winged ants could also be seen inside the nest.

Why did the ants of the terrace—my particular friends—live together with complete understanding, co-operating one with another and taking their food in common when I gave them bread or honey, while they fought savagely with the inhabitants of other colonies?

One fine day, my black friends of the terrace were attacked by a troop of large red ants with black bellies. I wanted to help them but was taken away to go for a walk. I was then seven and a half years old. When I came back I saw that the nest of my poor friends had been invaded by the red ants, which had driven the others away and were carrying off their cocoons. In my fury I poured boiling water on the reds, but all in vain. Then I followed them to their nest, about 40 or 50 feet away at the edge of a path. In their midst, I was astonished to find black ants smaller than themselves, just like my friends of the terrace, but living in common with them. Could these be slaves, hatched in this nest from cocoons which had formerly been stolen? Even then I put the question to myself, but was not able to answer it.

About the same time, in the same garden, I saw a large army of reddish-brown ants, all running in the same direction. I followed them, but they would not touch the bread or the honey I offered them. When they reached the wall at the edge of our garden, which I was forbidden to cross, they climbed it. I was much distressed. On their return they were laden with cocoons, and I saw them go back to their nest. I was surprised to find that this nest, too, was full of black ants, just like my friends of the terrace. And instead of fighting, the blacks took the cocoons and the red-browns occupied the nest in peace. For the moment I was astounded, and could not make it out.

Thus did I study the life of insects with all the enthusiasm of childhood—I was a scientist 'without knowing it,' like Molière's M. Jourdain with his prose.

My parents left Lonay in 1857, and I was sent to school at Morges, whence I often visited my maternal grandparents in the country-district known as "La Gracieuse." My grandmother, thinking that I was cruel to insects, induced my parents to forbid me to collect living insects. So I made a collection of dead ones, and continued to observe ants on the way between La Gracieuse and Morges. But my grand-uncle Alexis Forel, a naturalist, interceded for me about 1859, when I was eleven years old. One memorable day my grandmother brought me Huber's *Recherches sur les moeurs des fourmis indigènes* ["Studies in the Habits of Native Ants"], published in Geneva in 1810. The copy had been dedicated to her by the author. "There," she said, "I will make you a present of this book, written by my old flame Huber. He was not cruel like you, for he scolded me when I killed the ants that were eating my jam. I have never been able to get through his book. It isn't my style."

I did not merely read the book; I devoured it. I read it again and again. It was a revelation to me, and it became my gospel. Now I understood how my two Lonay ant-tribes, the red (sanguinary ant) and the red-brown (amazon) had enslaved my friends of the terrace (ash-black) ; I understood all about the eggs, larvæ, nymphs, cocoons, and the winged sexes of the ants, as well as their social customs and their wars. I even found that one of my observations, made before the age of eleven (Lestobiosis ; see Part IV), had escaped Huber's notice. Then I vowed to myself that I would be an ant-historian, like him, all the days of my life: and I kept my word.

Two or three years later, my parents bought some property at Vaux, three miles above Morges, and left me in lodgings, first at Morges, then at Lausanne, and finally at Zurich, where I took up medicine.

My principal studies in the habits of ants were made at

Vaux, but I continued them afterwards on my long holiday-journeys in distant countries, especially in America, Algeria, Tunis and the East. I do not wish to weary you, dear reader, with big words which claim to be learned, for true science is the enemy of big words. Nevertheless, we must come to some understanding if we wish to be intelligible. At the present time, more than 3,500 species and 4,000 races and varieties are known in the world of ants, or the myrmecological world (the old Greeks called the ant *Myrmex*). Pardon me, therefore, if in order to avoid inconvenience I use Latin names when I am not speaking of the commonest species, or whenever the English name is too complicated. Thus *Formica pratensis* is *Huber's wild field ant; Myrmica lævinodis* is one of the numerous forms known as the 'red' ants; *Lasius flavus* is the ordinary yellow ant found in Switzerland; and so on. Why should there be two names, you may say, or even three? Because the first is the name of the *genus* or small group or inter-related species, and the second that of the *special species*. To this last we often add the name of the race (r.) and the variety (var.); *e.g.*, *Formica fusca* r. *gelbaria* is Huber's ash-black slave ant, the one which lived in my terrace at Lonay.

All these ants are born from tiny eggs, consisting of a single cell, as with all living creatures. These eggs are transformed into *larvæ* (the white worms to which I alluded above), which later on become chrysalises or *nymphs* (the white, motionless cocoons mentioned above). These nymphs are sometimes, but not always, surrounded by a cocoon which they spin themselves from the silk formed in their mouths. Finally, the *adult ant* is hatched from the nymph.

But even in the nymphs, and more especially in the adult ant, there are extremely diverse forms in the same species, race or variety. We call this *polymorphism* (diversity of forms) of species. For each of the diverse forms we have in current usage a certain brief and very convenient sign, which we will employ for the sake of simplicity.

♂ signifies the male (Plate III, *k*).
♀ ,, ,, female (Plate III, *m*).
☿ ,, ,, worker or neutral (Plate III, *n*).

The workers themselves are often, but not always, subdivided as large, medium and small ☿. These three kinds differ more or less from one another. In extreme cases, the medium-sized worker disappears, and the large ☿ (Plate III a), very unlike the small one, is indicated by the symbol ♃ signifying *soldier*, although this 'soldier' often serves for quite other purposes than warfare.

In fact, with the ants as with certain other insects, namely termites (wrongly called *white ants*), the polymorphism of the species serves to *differentiate the work* of the individual members of the society. In the ants, the ☿ and ♃ are always derived solely from transformed females, but in the termites they are derived indifferently from transformed ♀ or ♂.

Organized division of labour is the essential condition of all life in a collective society. In the ants, it is the anarchic social instinct, innate and pre-ordained by a different heredity for each species, which compels each of their polymorphous forms to adopt its own specialized work. Heredity itself has been gradually crystallized in each species, during millions of years, into what is known as *phylogenesis*, that is, the gradual transformation of species in a way that can be followed in fragmentary fashion by the study of their fossil remains. The more or less extensive relationship of living animals and plants also bears eloquent witness to the same process. Races and varieties are capable of inter-breeding, of cross-fertilization ; true species cannot inter-breed. That is the distinction.

We men are fierce beings, family-loving individualists, endowed with a great brain and a desire to command and oppress weaker folk. Our sentiments of sympathy and devotion are as a rule very exclusive and scarcely social at all. But at the present time we cover the surface of the whole globe with *a single true species*, for all our living races and varieties can produce fertile cross-breeds between them. Thanks to modern means of transport, therefore, we can achieve something which the little ants, with more than 3,500 distinct species, each possessing its fixed instinct, are unable to establish—a world-federation of races. That is our only means of taming ourselves to any reasonable extent, and of putting a definite end to our wars, as the United States and the Swiss Cantons have done among themselves. When such a state of affairs becomes universal, we shall never repeat the horrible tragedy of the World-war of 1914-1918. But we shall still be oppressed by the age-long tragedy arising from the very fact of our individualistic nature, which makes us revolt against any social organization that restricts our liberty, and so demands communal laws. We shall see whether the social war begun in 1919 will be able to triumph gradually over our egotism in its fiercest manifestation—organized war between states.

Returning now to our ants : I propose to divide my book into five Parts, so that anyone who wishes may read one of them by itself ; these preliminary remarks being designed to give them the essential information. I shall, however, refer from one Part to another, for the benefit of those who wish to study the whole work.

I Genesis; Forms; Anatomy; Classification; Geography ; Fossils.

II Feelings; Physiology; Ants and plants; Guests; Parasites; Nests.

III Apparatus; Foundation of colonies; Behaviour in the nests; Cattle; Gardens; Parasites.

IV Alliances and wars; Parabiosis; Lestobiosis; Slavery.

V Special customs, Epilogue.

And now, dear reader, dive in among my ants, which will not sting you, never fear. Then when spring comes, or during your holidays, observe them in nature—in the fields, forests and mountains. Verify what I have written, and correct me where I am wrong. The only way by which science can progress is from corrected errors to corrected errors: I mean that science which is always modest in its observations and experiments, and which does not deal in long words and high-sounding metaphysical hypotheses. I guarantee you genuine enjoyment if you have the patience to observe well.

In closing, I must offer my special thanks to M. Erich Heinrich for his admirable illustrations, which are as much the fruit of love as of talent. Such illustrations make the ants live for the reader. The figure on the cover, suggested and designed by M. Heinrich, symbolizes the social services which ants perform for one another.

My gratitude is also due to my friends and colleagues, Professors Emery, Escherich and Wheeler, as well as to M. Bruch, who have kindly allowed me to borrow illustrations from their works. I am further obliged to my myrmecologist friends, Dr. Santschi and Dr. Brun, as well as to Messrs. Janet, Kutter, Wasmann, Viehmayer, Wroughton, Mann, Stumper and others, to whom science like myself owes much.

I must also express my indebtedness to Mme. Kündig, who publishes my work in Geneva, for all the help she has rendered me.

Auguste Forel.

Part I

INTRODUCTION

In spite of a justifiable dislike of far-reaching theories, all that they have definitely given us must be accepted. I assume that my readers are acquainted with the names of Lamarck, Darwin, Haeckel and others. And I also assume that, according to their temperaments and beliefs, they have already more or less given their allegiance in advance, to the one side or the other. But now it is time to lay aside all sentiment, and simply to distinguish the true from the false or the doubtful. That is what I am trying to accomplish by writing down nothing that is not a verified scientific acquisition.

Even the bitterest enemies of the so-called Darwinian theory—the Jesuit Father Wasmann, for instance—are nowadays obliged to recognize that animal and vegetable species are the result of gradual evolution. The idea that species were produced by a single act of creation can no longer stand when confronted by reality. Nobody knows how it all began—certainly not from a single cell, but by means of several, whose ultra-microscopic hereditary ancestors had existed everywhere. The element of all life, the *cell*, which is microscopic, is already a world in itself. This can be seen in figure 13, representing the cell of an ant-gland which forms and secretes a special chemical juice. This cell, peculiar to a group of species, represents in itself a very complex chemical laboratory, and it possesses in itself what we call the 'hereditary energies' of its species.

Energy was formerly defined as *latent force*, concealed, that is to say, in contrast to *living* or positively active force. Fundamentally, no one understands what is hidden behind all those energies or forces, live or latent, which set the world and ourselves into actual action (movement) or potential action (latent energy). These terms will not avail to cover our absolute ignorance of the first or metaphysical causes of the universe. But we cannot manage without them. To-day we speak of 'ions,' 'electrons,' etc., but these are still metaphysical hypotheses. We may leave them alone, like the 'atoms' which were supposed, some fifty years ago, to be indivisible and which are now believed to be divisible to 'infinity,' concerning which man cannot form any sort of idea whatever.

Heredity signifies those qualities in descendants which reproduce qualities of the ascendants from which they have sprung. Now the primæval source of the ascendants is lost in the darkness of time, and the further back it stretches, the less will the descendants resemble their ascendants thus multiplied. As no single man, nor even a single ant, is absolutely identical with any other, it follows that heredity, far from being inevitable, is only more or less relative, and that according to its degree. The greater the extent of cross-breeding, that is to say, diversity between races and varieties which mate with each other and produce healthy and fertile offspring, the more their descendants will vary. But the truly different species are those whose germs can no longer combine to give rise to fertile offspring, because they act like poison upon one another, and these species will gradually become fixed by reason of that very fact. Thus far we can claim scientific certainty. Hence, as other facts show that it must have taken hundreds of thousands of years for a *true species* to be clearly differentiated from others, it follows that a similar lapse of time is required to change *entirely the heredity of all that can no longer be crossed or modified by individual acquisition or education, or even deteriorated by germ-poisoning*, which I have myself christened 'blastophthory.'

Haeckel and others imagined that the animal and vegetable cell which they regarded as primitive issued directly from a form of inanimate matter. This was a strange illusion. Small as the cell appears to us, it is none the less a complicated world. No one has hitherto been able to trace its heredity, and it conceals a world so tiny as to defy our most powerful microscope. And so we must learn to hold our tongues when we are unable to find out the truth, and not veil our present ignorance of the origin of life under stupid hypotheses in terms of *vitalism* or *mechanism*. I will spare you all that, friend reader.

Darwin was much more cautious and scientific than Haeckel. To the latter, however, we owe a clear distinction between the origin, that is to say the *genesis of species* through ascendants, which he calls *phylogenesis*, and the genesis of each individual, that is to say its development from the egg stage to the adult stage, which process he calls *ontogenesis*. He claimed that the ontogeny of each individual was an abbreviated recapitulation of its phylogeny. There is an element of truth in this opinion : but we must beware of making it into a dogma, for it has too many exceptions.

Nevertheless, science has advanced since then. Darwin demonstrated the struggle for existence among living creatures, and natural selection of the strongest, the most enduring and the most fertile. At the same time, he already understood that characters acquired by external influences must eventually be capable of transmission if they were repeated in several generations. De Vries afterwards confirmed this fact, and apparently deduced from it his sudden mutations of *species*, which he proposed as a new explanation of the evolution of species, preferable to transformation by natural selection by reason of its greater constancy.

Since then, Ewald, Hering and Semon have shown the facts in a more definite light. Hering, in his monumental phrase, declared that Instinct is the memory of the species, and Semon in his theory of Mneme had the wisdom to take human beings as they are, without desiring to probe into their origin to an unnecessary extent, and studied the effects which stimuli from the outer world (sounds, light, smells, touch) produced upon them and their senses. He then studied the reactions of living beings to repeated stimuli of this kind, and the manner in which they stored them up as *engrams* (memories in the whole of their cells and more especially with the aid of their senses). Repetition with the aid of *mneme* (memory on the broad sense) of a complexity of engrams is his *ecphory* (rememoration). By reason of the true heredity of characters acquired and gradually accumulated by repetition, instinct is for the species what acquired memory is for each individual. Semon also gave irrefutable proofs of the gradual heredity of certain acquired characters, for example those found in the sole of the human foot.

Habit, in our own case, becomes gradually unconscious or, more exactly, subconscious through repetition, and ends in becoming so exact that it resembles inherited instinct. We shall speak of it in connection with the ants. And yet, however automatic it may become, every habit has been individually acquired, thus differing radically from instinct inherited from ascendant ancestors.

Another general law teaches us that the brain is the organ of our intelligence, our feelings and our will, in short, of our mind. This same law obtains in all the higher and intermediate animals, including ants. The brain is also the organ of instinct. The larger it is, relatively to the size of the animal, the more developed is the mentality. But a small body which is complicated requires proportionately more nerve-cells than a large body of the same degree of complication, for the group of cells necessary for the same function—that of sight, for instance—is more or less identical in the two cases. With its unequal size for an equal function, the small animal's brain is therefore larger, *relatively to the weight* of the body, than that of the biggest.

At this point, I may refer the reader to my book on Psychic Activity* (Anatomy, pathology, hygiene) where all who desire fuller information on the matter can obtain it without undue trouble.

Here, however, I must continue with my story. We men, like all vertebrate animals, have our bony skeleton inside, whereas the insects have theirs outside. In their case it constitutes a skin, which is generally very hard and surrounds the whole body, forming joints, such as we have in our bones. This skin is called chitin. In the Crustacea (crayfish, lobsters, etc.) it contains lime. These animals, then, have no bones ; nearly all their internal organs are soft. It follows that the muscles by whose aid they move as we do are attached to their outer skin of chitin or lime, which is their equivalent for bones.

My little friends the ants constitute a *family* of insects belonging to the great *order* of *Hymenoptera*, which also includes the humble-bees, the wasps, Bembex, whose habits Fabre has described so well, and many others. Although

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* *L'Activité psychique* (Kündig, Geneva, 1920).

social like the ants, the termites belong to quite a different order—that of the Neuroptera whose metamorphoses (changing of the skin and other ontogenic transformations of the individual) are incomplete, whereas they are complete in the Hymenoptera, as in the butterflies with their caterpillars and their chrysalises.

Let us then lay aside all sweeping theories while we describe the evolution and the bodies of our ants. Part I will be divided into seven chapters: Chapter I, Phylogeny; Chapter II, Ontogeny and polymorphism; Chapter III, External anatomy; Chapter IV, Internal anatomy; Chapter V, General classification; Chapter VI, Geographical distribution of ants throughout the world; Chapter VII, Fossil ants.

Chapter I

PHYLOGENY OF ANTS

Ants have certain near relations among the Hymenoptera which bear a great resemblance to them, though the females are *apterous*, which means 'wingless,' the males alone being winged ; nevertheless, these near relations are not social, and live alone. In passing, I may beg the reader to make a mental note of the terms printed in italics (*e.g.*, the word *apterous* above), which I have explained to them or which I will explain when they appear, for these terms are indispensable to our mutual understanding.

The term *phylogeny* has already been explained. The Biblical Genesis claimed to deal with the Universe. We will here content ourselves with that of the ants. Unfortunately, most of the few genuine fossil ants known to us are winged, and are related to all the sub-families (see Chapter V) still alive ; and they throw no light on the problem of their primitive phylogeny. As yet we have not discovered any 'pre-ant' which resembles our present *Mutillids*, the nearest relations to our ants. But the Mutillids, although much compressed between the thorax and the abdomen, have not that narrow pedicel, consisting of one or two joints which the ants possess. Nevertheless, my friend the late Henri de Saussure, who had a very wide knowledge of the Hymenoptera, would insist that a male of the ant-genus *Mystrium* found in Madagascar was a Mutillid, and I had a lot of trouble in proving to him that he was wrong. Now *Mystrium* is a genus of the *Ponerinæ* (Ch. V) which I consider very primitive (see its head in fig. 3 *A*).

All the five sub-families are represented among the fossil ants known to us. But we have other land-marks besides fossils, whose preservation is always very precarious, especially in the case of little insects so lacking in solidity as the ants.

In the first place it is perfectly evident that the ants must be derived from non-social insects very closely akin to the Mutillids, whose females probably had no wings. Indeed, the ♀ of all the present-day ants have very *caducent* wings, that is to say, they fall very easily and are entirely lacking in some genera.

Furthermore, in my opinion, four of the five sub-families of ants are directly descended from the fifth, the *Ponerinæ*, through intermediate forms which differ in each case. True, my friend Emery thought that the *Dorylinæ* are older than these, though only as a specialized branch; but for my part I could not agree with him. You will smile at our differences, dear reader; but, as you know, it is the clash of ideas that strikes out the spark of truth. Perhaps one day they will find the 'pre-ant,' as they have recently found the curious new quadruped 'Okapi,' and perhaps it will not be quite Ponerine nor quite Doryline, or unlike both of them! And so we will wait. Above all—no dogmas.

Further evidence of the antiquity of the Ponerinæ is to be found in their social habits, which are elementary and little developed, in their gizzard or 'pumping stomach,' which is primitive and not yet specialized, and in the fact that their larvæ can eat without assistance the food given to them. These are important indications, which combine to show the beginnings of a social life, becoming more and more complex in the other sub-families.

But we find in the ants yet other examples of phylogeny in detail which are very instructive. The general geological history of the earth shows that the continents have not always been as they are to-day, and that their climate has varied in the course of the terrestrial ages. Old continents have disappeared. Others have been flung up. At an epoch known as the *Quaternary* (the nearest to us !), in what we call the *Glacial Period*, which goes back to the period roughly from 1,500,000 B.C. to 500,000 B.C., fossil man already existed, but the cold had so overwhelmed our earth that it had destroyed nearly all the living creatures in our own region, relegated our animals and plants to the far south, towards the north of Africa, and reduced what still remained of the splendid fauna and flora of the preceding epoch, known as the *Tertiary*, to a narrow limit around the Equator. It was not until after the Glacial Period that our earth was gradually warmed anew. The zone of tropical plants and animals then grew wider again, and as the glaciers disappeared, living beings, adapted to temperate climates, reclaimed part of the northern territory in our hemisphere and part of the southern territory in the other. Geology offers clear proof of this. There followed an indeterminate period, a little warmer than our own. We shall mention this again shortly in connection with the ants of the fauna known as *xerothermic* (warm and dry).

Before the Glacial Period, Europe, Asia, and North America were united by Greenland, Iceland, the Faroes, Spitzbergen, the Aleutian Islands and Alaska, and evidently had about the same general temperate flora and fauna. For the world was then so warm that living beings from our own parts could journey to what we call the Polar regions. The

Glacial Period afterwards entirely separated those of North America from those of Asia and Europe, but whereas the rich pre-glacial flora and fauna in America could withdraw without overmuch inconvenience towards Texas and Mexico, part of that belonging to our region was drowned in the seas (Mediterranean and others), or parched up in the deserts of Arabia or the Sahara, or held in check before the lofty Himalaya and Burmese Mountains, etc. This probably explains why only the strongest and most widespread races were able to live in the temperate zone of the Old World, and hence why the present flora and fauna of North America are so much richer than our poor products known as the *Palearctic* flora and fauna of Northern Europe and Asia.

One very clear fact cannot be overlooked ; the North American species mostly resemble our own to such an extent that we can often only divide them into races. Nevertheless, *all* of them are sufficiently different to be clearly distinguished. We might almost say that anywhere in North America five to ten kinds of "imitators" can be found, all different from our European species. This is the case with oaks, butterflies and ants, and also with other terrestrial animals and plants ; nevertheless, North America has in addition special local forms which we lack, whereas the converse is much rarer.

Does not this singular fact furnish irrefutable evidence that since the Glacial Epoch flora and fauna which were previously common to North America and the Old World have begun to evolve, that is, to change their forms, especially in North America, each on its own lines ; but that these 500,000 years or more have not sufficed to render the differences between them any greater than those between species closely akin, or races. At the same time there are three exceptions which serve to confirm the rule. (1) Certain special forms which were evidently already localized in various countries long before the Glacial Period; (2) species recently imported in ships; (3) some forms found near the North Pole. We shall speak of these in Chapter VI, in connection with geography.

But there are yet other interesting facts confirming evolution and climatic changes. Iceland, like Greenland, despite its relatively mild climate, contains no ants. I have duly confirmed this fact from the testimony of a reliable Icelander. Now not far from the North Cape in Norway, that is to say in a place much colder than Iceland, five species of ants are to be found, and have been sent to me to identify. How does that happen? Simply, I believe, owing to the fact that Iceland, being separated by the sea from the Continent and being visited by only a few well-warmed steamers has, like the south of Greenland, never been repopulated with ants since the Glacial Period. I will guarantee that if anyone were to amuse himself by transporting thither some fertile females of our *Formica fusca* or *Lasius niger*, Iceland would soon be populated with them, for the first of these species can reach the North Cape and live in the Alps at a height of nearly 10,000 feet.

We have just alluded to the fauna known as xerothermic. I will explain this by taking a typical example which I observed very carefully myself, during the time I spent among the ants in my youth at Vaux near Morges. Behind the old castle of Vufflens, the abrupt ravine of Morges in front of Vaux forms several steep slopes, entirely exposed on the south and absolutely protected against the wind on the north. There, and there only, are found some of the southern species (among others *Camponotus æthiops* and *lateralis*) for which one may seek in vain in the rest of the canton of

Vaud, save in one or two similar places, though they occur in Valais, Ticino, Italy, etc. How did they get there ? We find another phenomenon like this in Stein am Rhein, in the canton of Schaffhouse, and in other specially sheltered spots, in Germany and other parts of Europe. Nowadays we explain the matter by assuming that after the Glacial Period our climate began to grow warm again until the temperature was slightly higher than that of to-day. The southern species, which then travelled a *little further* north, would have left behind them a sort of local residue in the sheltered places, sun-parched and dry, and hence described as xerothermic. Indeed, the phenomenon is so widespread, according to reliable observers, that it calls for a general explanation. The nuptial flight of the two *Camponotus* species of Vaux mentioned above is too local and takes place at too low an altitude for us to assume that fertilized ♀ are transported to such great distances as those separating Vaux from St. Triphon or Fully in Valais or the Salève, as well as other localities with xerothermic fauna. Again, certain species of ants commonly found in Ticino and throughout southern Europe (*e.g.*, a *Pheidole* and a *Cremastogaster*) are not found in the warm part of Valais, between Fully and Sion, although they could live there perfectly well. For my part I am persuaded that the species encountered near Lyon, for example, could not have passed round the Alps by Geneva since the Glacial Period, and that this is also the reason why we do not find them in any of our localities with xerothermic fauna. Perhaps one day the Simplon Tunnel will bring them to Valais.

Another very important case is that of the great tribe of *Attini*, or fungus-growing ants, which we shall describe later on. These singular insects, with their very special habits and forms, are found exclusively in tropical America.

Only one of their numerous species has become adapted, evidently by a gradual process, to the climate of North Carolina and some of the other States, with a more even though somewhat warmer climate, in the middle of the United States. The *Attini* (see the head in figure 3 *G*) differ absolutely from all other genera of ants found in America and the other continents. A single ant from Sumatra and others from America, related to the smallest *Attini*, resemble this tribe and certain other ants of the Old World ; but *none of them grow fungi*. Now it is only the large and medium sized genera of *Attini* which cut off leaves from trees to feed the fungi : the little ones feed them on manioc, the excrement of worms, caterpillars, etc., their gardening instincts being less highly developed and sometimes only temporary. From these facts I have concluded that the following hypothesis is very probable.

The instinct for growing fungi began in tropical America, *after* the total separation of that continent from the others, and first showed itself in the small species, similar to certain of their present-day relations which are fond of rotten wood and the fungi it favours. In this region their instinct for eating fungi and then taking steps to grow them probably began in very early geological periods.

But it was only by slow degrees, in the course of vast stretches of time, that this instinct was perfected to the unprecedented point which it now attains in the large species. And simply because of the fact that they began to cut leaves which furnished them with a superabundance of nourishment, the large *Attini*, whose instinct for the cultivation of fungi is most fully developed, increased in size more and more.

Dear reader, do not laugh at me now that I too am found indulging in hypotheses, and remember this one when we speak of the *Attini* in Part V. I have thought over the matter to no purpose—I have not succeeded in finding another natural explanation for the phylogeny of the *Attini*, which is calculated to excite curiosity in us all. On my hypothesis, the development and form of the body are in perfect agreement with one another and not only with those of instinct, to such an extent that as early as 1892 I came to the above conclusion as to the phylogeny of the *Attini*, before I knew of their cultivation of fungi. I only learned of this in 1893, thanks to the memorable researches of Möller.

Various reasons lead geologists to suppose that there was once an Antarctic continent (*i.e.*, in the extreme south) which was afterwards submerged in the ocean. It is indeed singular that very similar species, or rather species which bear a real relationship to one another, are found in the southern extremity of America, in New Zealand and in the south of Australia. A glance at the map of the world will show how great a distance separates the continents south of the Equator from one another. Yet there is no doubt about the relationship of creatures living so wide apart, in ants as well as in other animals.

But things are further complicated by what is known as 'convergence,' which sometimes plays strange tricks upon us. Indeed cold has the effect of making colours duller and forms, on the whole, more monotonous, while conversely heat and sunlight make the first more vivid and the second more varied. As a result, species living near the South Pole often bear an *external* resemblance to those in the North Pole, although there is no real relationship. Thus it was that my friend Gustav Mayr, an excellent myrmecologist, came to connect certain Chilean ants with the genus *Lasius*, which is only found in North America, Europe and Asia ; appearances had misled him. Dissection afterwards proved to us that all the false *Lasius* of the Southern Hemisphere have gizzards entirely different from those of the true *Lasius*, and that they are all really akin to the Australian genus *Melophorus*, and the New Zealand *Prolasius*.

In fact, terrestrial animals which are not able to endure the tropical climate cannot cross the Equator unless they are borne by a swift steamship, and they could not do so at all in olden days. And at any rate as regards the ants, those of the two hemispheres are certainly radically different. It is not quite the same with the tropical genera, certain species of which were gradually transformed and adapted, during the geological periods, to temperate or cold climates.

But even this confirms our theory, for at least those genera of ants which adapted themselves to the cold or temperate regions of the south are *unlike* those which adapted themselves to the north. The enormous tropical genera, *Camponotus*, *Pheidole* and *Cremastogaster*, have many representatives in the temperate zone of the Northern Hemisphere, but none in the Southern. On the other hand the tropical genera *Monomorium* and *Dorymyrmex* are represented in the Southern Hemisphere and scarcely ever in the Northern (only in the region we call sub-tropical). The genera *Lasius*, *Formica* and *Myrmica* live only in the north temperate zone, the genus *Huberia* is peculiar to the cold region of the Southern Hemisphere, and *Orectognathus* and *Melophorus* to the cold, temperate, sub-tropical and tropical regions of the same hemisphere, etc.

Pardon these details, dear reader, but I am trying to prove to you that the evolution of species does not rest upon hypotheses alone, but mainly upon real and incontrovertible facts. Special examples, like those connected with the ants, prove it in the details of their phylogeny. And here, as we have just seen in dealing with the *Attini*, habits and instincts, inasmuch as they are functions of the brain, have no less value than the form and anatomy of the body.

For example : near the convent of New Athos, on the shore of the Black Sea, Rehbinder found *Strongylognathus Rehbinderi*, a species to which we shall again refer in our fourth volume, capturing nymphs of *Tetramorium cæspitum*, as our Swiss amazon ants do. This creature has the same sickle-shaped, pointed and toothless mandibles as our amazons. But it is related, through a series of other intermediate species, to *Strongylognathus testaceus*, which is itself no more than a vile parasite upon this same *Tetramorium*, the fertilized female coming and living with the female of *Tetramorium* like a cuckoo. Only the offspring of the latter labour to bring up the two species. Thus the worker of *S. testaceus* has become useless and is gradually disappearing, though not quite gone yet. Now when we induce stranger ants to attack a nest of mingled *S. testaceus* and *Tetramorium*, we may observe the little ☿ of *S. testaceus* fighting like the amazons and struggling, sometimes without success, to thrust their sharp pincers into the enemy's head. This is an atavistic reminiscence which has become useless, a veritable caricature of the ancestors' actions, due to the *hereditary mneme of the species* in instinct. "Instinct is the memory of the species ! "

The forms intermediate between *S. Rehbinderi* and *S. testaceus* are all less definitely slave-makers than the first, and appear to have already attempted some degree of parasitism in their ♀. But we have still to make new and more precise investigations of their habits. In any case it appears to me beyond all doubt that parasitism and the degeneracy of the worker in *S. testaceus* are *secondary*, that is to say, they are the *result* and not the *phylogenetic origin* of the slave-making habits of their ancestors. This being so, there is also no doubt that the slave-making ants are derived, also phylogenetically, from worker ancestors, for the sanguinary ants, for example, provide us with all the transitions between the complete worker and the more or less incomplete slave-maker. In this case, therefore, phylogenetic filiation passes from normal social work to parasitism by way of slave-making. But we must beware of generalizing, for other genera, facts which are perfectly true for *Strongylognathus*. We shall realize this later.

The preceding sketch has shown that our present acquaintance with the phylogeny of ants is only and can only be very fragmentary. But these fragments increase more and more with the aid of patient research. Moreover, they consolidate and complete each other like the scattered remains of a fossil skeleton, and help us to reconstruct, bit by bit, the early genealogy of the Formicidæ, represented by its phylogeny.

My readers will understand that the comparatively recent extremities of the branches of the genealogical tree are easier to deal with than the branches themselves, or more especially the old trunk. In fact, the deeper we try to plunge into the fossil geological epochs, the more hypothetical and uncertain does everything become. If our earth in the beginning was boiling hot and even on fire, living beings such as those we know could not have lived on it. Since every known living cell already has a 'specific heredity,' we pointed out above that this heredity must have been caused by the ultramicroscopic life of a 'sub-cell' which no one as yet knows. That would be the actual trunk of life, but as to this we can only frame empty hypotheses. It would be better to say nothing on this subject. But we already know that plants and animals are connected with one another at their common phylogenetic base by living beings composed of one cell, microbes which are sometimes almost as much plants as animals. As for the origin of life itself, let us wait until we know more than we do at present before discussing it.

As we trace back the tree of life with its two branches, the animal and the vegetable, we see more and more clearly into its phylogeny, but this is still often very obscure. We have already discovered this with regard to the ants, since the 'pre-ant,' related to the present-day Mutillids, is still entirely unknown to us. On the other hand, we have several series of detailed facts (the connection between North America and the Old Continent, the *Attini*, *Strongylognathus*, etc.), where filiation can be recognized even in far-off ages.

In the following chapter we will leave theories and hypotheses and come to concrete facts.

Chapter II

ONTOGENY AND POLYMORPHISM OF ANTS

ONTOGENY

We said in the introduction that the cell is a little world, though it is often invisible to our imperfect eye. Now every egg, as we saw in the Preface, is in the first place a single cell and yet contains potentially, in hidden (latent) energy, the whole life of the adult individual that comes out of it, whether that individual be a man or an ant. The progressive development of latent energies in each species is called its ontogenesis.

But it is not solely and invariably hereditary energy or latent force which brings about these successive transformations in animal life. Further influences from the surroundings in which the living thing is developing—its food, etc.—combine with it.

In man and the higher animals, every young creature is born from an egg fertilized by another cell, that of the male. The latter are extremely small and are known as spermatozoa in these and all other animals. This is a very long word for anything so microscopic, and yet this little thing contains exactly the same amount of the substance called chromatin, which determines the paternal heredity of the parent, as the maternal egg or ovule, which is much larger. We have indubitable proof of this in the fact that on an average our children resemble their father as much as their mother, although the latter bears them in her womb for nine months and feeds them even longer. Furthermore, the matter has been directly proved by the microscope, through which we see the spermatozoon, which has entered the egg in order to fertilize it, begin by absorbing some of its substance called *protoplasm*, and then supply exactly half of the chromatin of the *nucleus* which is embedded in this protoplasm.

All the same, there are animals which can reproduce themselves for a long time by 'parthenogenesis,' that is to say their virgin female and, in the case of the ants, her derivatives the workers, can reproduce themselves by laying eggs which are not fertilized, or in other words, which have not come in contact with spermatozoa. This is the case with ants, bees, wasps and many others. Here the gentleman can be dispensed with, but he can never dispense with the lady if he wishes to have progeny. Still, in the long run it seems that parthenogenesis does not suffice, and eventually leads to the extinction of descendants, unless at some time fecundation by a little cell, male or otherwise, occurs to bring about a crossing of different individuals.

In fact, even in plants, microbes and animals composed of a single cell, one of these cells often becomes attached to another and exchanges with it half the chromatin of its nucleus. This is a sort of *elementary mating*. So it seems that after all the gentleman is required from time to time to strengthen life, but the lady can sometimes (not always) produce offspring unaided for a fair time, even when there exists a male differentiated from the female, which is not the case with microbes. So you see, friend reader, that matters are complicated, and a magical 'big word' does not explain everything ; but you will find that there is a good deal more to be said, and that the deeper we dive into things the more complicated the problem grows, instead of simplifying. Do not forget that *the hereditary energy latent in an egg or a seed, whether fertilized or not, is different for every animal and vegetable species.*

We have spoken of polymorphism in the ants and termites. In bees also, the ♂ differs greatly from the ♀ and there is a ☿ derived from the ♀ or sole queen by *phylogenesis.* Now Dzierzon once proved that if the queen-bee dies, the ☿ are capable of transforming a ☿ larva, not more than a few days old, into a *queen or* ♀. All they need to do is to enlarge its cell and modify its food. *In bees,* therefore, ontogenetic differentiation between ☿ and ♀ only takes place when the larva is still young; it never happens to a full-grown larva. Certain minds which are disposed to generalize everything by hypotheses jumped to the conclusion that the same thing obtained with ants and other creatures, although ants have *neither special food nor special chambers for their larvæ. They are wrong. Polymorphism in ants takes place in the egg.*

Parthenogenesis among bees has been proved, but their unfertilized eggs appear to produce ♂ only. I have demonstrated parthenogenesis of a similar kind in ants, when ♂ alone were hatched from the unfertilized eggs. At a later date, however, Dr. H. Reichenbach proved that sometimes ☿ are hatched from them.

The strangest case of all is that of the termites, whose ☿ and ♃ are sometimes derived from the ♂ and sometimes from the ♀, whereas those of the ants always have small ovaries. In 1912, Professor E. Bugnion, who had made an exhaustive study of a species of termites in Ceylon, clearly proved that the horn of the ♃, even *an entire* ♃ *in miniature, was already completely formed when it came out of the egg.* This is his own description, and he gives an illustration of this embryo. Furthermore, in 1910 Bugnion had dealt with the question in connection with other insects, and shown that in general their sex is only determined on fertilization. To the male substance of *chromatin* he gave the name of *spermie*. Chromatin is the source of heredity, and in short Bugnion concluded that 'spermie' which is rich in chromatin determines sex on the female side and 'spermie' poor in chromatin leaves to the ovules the power of determining sex on the male side. There is, in fact, a cross-effect. When the female chromatin of the egg is strong and predominating, a ♂ is generally produced. But we have just seen that this is not *always* the case. Bugnion nevertheless explains the matter by means of other still more complex investigations, which I will spare you, friend reader.

Summing up, therefore, the *moment of ontogeny*, when the sexes and the polymorphic forms of offspring born of the same parents are differentiated, varies according to the species, genera and families, and we can never establish a general dogma which will have the force of a law.

But here we come to a very different state of affairs. In 1864 or thereabouts I captured from a bush some thirty little caterpillars, still black, belonging to the beautiful moth, *Saturnia pavonia minor*. I left the rest on the bush, and shut up my spoils in a large, dark box (which I still possess to-day), and fed them very carefully. It is known that after their skin is cast for the fourth time, the caterpillars of the little moth become green all over, the colour of foliage. Now my caterpillars in their dark box *all* kept a large black transverse band on each section of their bodies until the moment when they entered the cocoon. Some of them remained almost entirely black. At the same time, their sisters which were left on the bush all became green all over after their fourth moult. I was astounded, and even then I rightly attributed this difference in colour to the darkness in which my prisoners had been living.

Later on, Standfuss and Fischer made experiments with various butterflies under the action of cold, heat and light, which have become classic. For instance, they submitted the caterpillars and chrysalises to the prolonged action of cold, and the result was a darker colouration in the butterfly, with large parti-coloured spots and even a different form; the action of heat, on the other hand, rendered the colours brighter and gayer. They proved, moreover, that if the experiments were continued for several generations, these unforeseen changes might be transmitted to a future generation, which need not in its turn be submitted afresh to the action of cold, for example. They had been transmitted, therefore, by the action of the hereditary mneme—in a transient fashion, at any rate.

These facts were afterwards confirmed, and the term *variations* has been applied to changes like this, due to the direct action of an external agent upon the ontogeny of a species. A variation, therefore, is not the same thing as a true variety, whose characters are primarily hereditary. But as it becomes gradually fixed, a variation may become a variety. There are abundant variations in the humble-bees and butterflies, for example, but few in the ants.

In his laboratory at Vienna, the late Paul Kammerer caused salamanders to vary in this way from yellow to black, claiming to have confirmed the acquired heredity of certain variations by systematic repetition, for several generations, of the action of the external agent which had produced them. On these lines, by means of the constant action of light he even succeeded in producing eyes in a blind cave-animal, Proteus (*Proteus anguinus*), which he showed me. The normal Proteus still has the rudiments of the optic nerve possessed by its ancestors, which were able to see. These rudiments were reconstituted under the prolonged action of light during several generations.

Hence, although in general the course of ontogeny is predetermined for each species by its own heredity, certain *additional* modifications result from the repeated action of the environment, and these modifications react on the latent hereditary *energies*. But it is evident that they are not deep, and are destined to disappear after a few generations, as soon as the agent which produced them ceases to act. Then in their place the ancient energies of the species, anchored for hundreds of thousands of years in the deep hereditary mneme, will reappear as was explained in the introduction.

Science does not pause on such a promising road, and now in the twentieth century we have chemistry appearing on the scene. Before this, the Swiss surgeon Kocher had proved that the evil effects of goitre could be counteracted or arrested by grafting into the patient's neck the normal human gland known as the *thyroid*. In 1903 Bouin and Ancel, Steinach, de Goodale and Lipschütz proved decisively that if male sex-glands were grafted upon a female and *vice versa* at the moment of puberty, a little before or even a little after, the ontogeny of sex could be modified as follows :

Whereas simple castration produces a being neutral from the sexual point of view (as in oxen, capons, etc.), Steinach showed that by grafting testicles upon a female animal he *made it masculine* and by grafting ovaries upon a male, he *made it feminine*. And he found that not only the hair, feathers, size, bone-structure, etc., but even the direct sexual instinct is *feminized or masculized*. The hen acquires, in some degree, the feathers and spurs of a cock, the Indian boar acquires teats and suckles the young, etc. The corresponding sex organs are developed or atrophied, according to the sex of the gland which is grafted.

Again: Steinach and Lichtenstern grafted upon a male invert who had been castrated and whose body was distinctly feminine in character, a testicle from a normal man, which had been removed during an operation. The result was that this invert (homosexual) was rendered entirely masculine, not only in body but in sexual appetite and the corresponding mentality. These experiments are of supreme importance in connection with the ontogeny of the sexes in all animals, and throw an entirely new light upon it. They prove that the nature of the chemical laboratory constituted by a gland (see fig. 13) may react upon the whole body—and even, if grafted in time, upon its ontogeny.

Although, therefore, it is true that phylogeny is the great primal cause of ontogeny in each individual, the physical and chemical influences acquired in the course of this ontogeny partially revenge themselves by reacting on the phylogeny of the species.

It was all the more important that we should not neglect such important facts as these inasmuch as we shall have to return to them in Part II, in connection with hermaphrodites and pseudogynes (figs. 33, 42, 43 and 44 in Part II). Everything may occur in nature, but nothing in it is absolutely identical; the shades are infinite. And now let us return to our ants, whose ontogeny will not surprise us.

In actual fact, *every phase* in the ontogeny of a species has been adapted to the various special ends of its life during the course of its phylogeny. If certain caterpillars that live on willows and poplars have an alarming appearance and two tails in the form of a whip, the reason is that these appendages have been adapted gradually *in the course of* *their phylogeny* to their ontogeny, in order to drive away winged parasites which sting them while they are caterpillars in order to lay eggs in their bodies : it is not for the sake of the beautiful moth which will arise from them. If the worker of *Strong. testaceus*, mentioned in our first chapter, is about to disappear in spite of possessing the ridiculous vestiges of its ancestors' slave-making instinct, its disappearance is not a freak of nature, as was formerly supposed, but is due to the fact that the parasitism of its fertilized female has rendered its existence entirely superfluous. We can see this in connection with other genera of parasitic ants, in which the worker, for the same reason, has entirely disappeared; and so on.

We must admit at once that the detailed anatomy of the eggs and larvæ of the ants still remains to be studied, so that rather than hazard crazy hypotheses we will skim rapidly over the subject. The ant's egg (fig. 1 *D*) is very small—a white speck, more or less elongated. Probably it already enshrines, potentially or in its structure, like that of the polymorphic termite, the differences of the various forms which will arise from it ; but this is not yet proved. Above all, it must not be compared with a hen's egg at the moment when the chicken comes forth. Before its fertilization, the hen's egg is fairly small. But whether it is fertilized or not, it afterwards grows enormously owing to the formation of a large mass of food *at its sides* (the yolk and white of the egg), destined later on to feed the real little cell, which is fertilized by the cock. And it was this cell (not we humans) which, before and during the incubation of the hen, was meant to eat first the yoke and then the white of the egg, developing its ontogeny meanwhile by innumerable divisions and by the differentiation of the embryonic cells into various organs, until the chicken was hatched.

The little creature then breaks the shell which has long ceased to have any connection with the primitive egg, but which encloses an embryo already mature and disposed by hereditary instinct to peck at grains of corn with its beak. Hence it is quite different from the primitive egg. Except with regard to the food of the embryo, the phases of the termite's egg bear some resemblance to those of the hen's egg. But for all we know, the anatomy of the ant's egg may still have some surprises in store for us. Pierre Huber, indeed, proved that ants' eggs, which are opaque when newly laid, *grow*, become transparent and curve over at one end before they are hatched, a fortnight or so later. Thus it is evident that they are transformed, probably by reason of the food which may be conveyed to them through their skin by the ☿, by means of endosmosis.

The egg-laying season of ants varies greatly according to the species. Some of them first lay ♀ and ♂ eggs in the spring, and then worker eggs ; others in summer, others in autumn. In the last-mentioned case, the offspring generally sleep through the winter as eggs or small larvæ, like the adult ants themselves, at the bottom of the nest. The ☿ take the eggs away from the fertilized ♀ immediately after they are laid. The duration of the time when they remain in the egg-stage appears to vary from two to about six weeks, according to the genus and the temperature.

Fig. 1 *D* represents some new-laid ants' eggs. Their fertilization, if it takes place at all, does not follow directly upon mating, but later, at the moment of laying, in a 'seminal vesicle' placed below the ovaries, near the posterior orifice of the abdomen. This orifice is called the *cloaca*, because it serves all purposes—for fertilization and for eceiving the secretions of the intestines, as well as for the poison and anal glands, of which we shall speak later. The seminal vesicle can be seen in fig. 19 *D*.

In order to understand the matter it must be explained that ants only mate once in their 'nuptial flight,' which takes place in the air, and which will be pictorially represented in figure 71 (Part III). Now this single mating process is usually accomplished in a few moments with several successive ♂, each of whom pours his semen into the seminal vesicle of the same ♀. The result is that this ♀, which lives a very long time, remains fertile for several years without mating again. The eggs she lays touch the spermatazoa in their passage towards the orifice of the seminal vesicle. Thus we might almost say that after the death of the male, which lives only a few days, the fertilized ♀ becomes a *kind of secondary hermaphrodite*, which fertilizes itself. That is a point of capital importance, which explains one side of the social life of ants and is illustrated in fig. 19.

Once again, dear reader, you see that living nature employs a thousand different means to attain the same ends. And we shall see many more of them yet. No one has hitherto been able to prove whether *all* the eggs of a fecundated female ant are fertilized when they are laid or whether some of them are not. In contrast to this, another member of the Hymenoptera, a relation of the bees, the Osmia so admirably described by Fabre, *before laying*, constructs small cells for its little ♂ and larger ones for its big ♀. It seems to me obvious that Osmia fertilizes her ♀ and does not fertilize her ♂ eggs, and that she does this at will by opening or closing her seminal vesicle, as the case may be, by means of its muscles (see fig. 19 *B* and *D*). But as the ants do not construct any cell for their progeny, they do not supply us with any indications which help to clear up the matter.

Ant larvæ have about twelve segments. They are illustrated in fig. 1 : *A*, *B* and *C*. These three figures differ widely from one another and partly correspond to the phylogeny of the sub-families of ants. Indeed larva *A*, which is long and very mobile and which has a skin covered with tubercles and a well-defined head furnished with mandibles or nippers, belongs to the primitive sub-family of ants known as the *Ponerinæ*. Their social life is on the whole less complete, less differentiated, less social than that of the others, and consequently their larvæ are less absolutely dependent on the ☿.

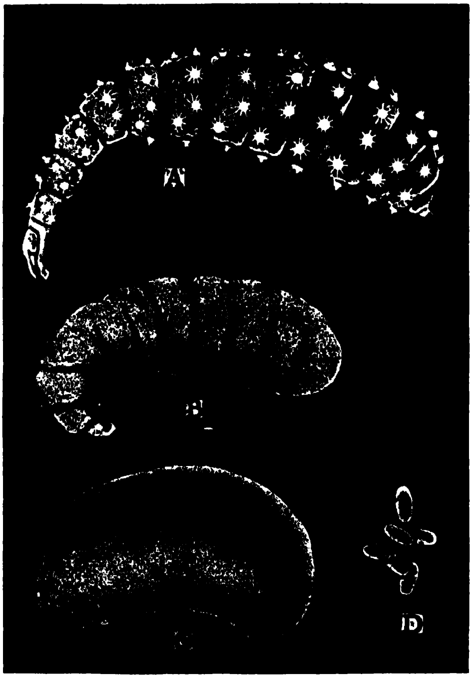

Fig. 1*

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* For the explanation of all these figures see the end of the Volume.

Wheeler in particular has shown that ☿ do not regurgitate the contents of their own crops to the larvæ, but that they merely place beside them dead insects or other food which the larvæ can afterwards eat on their own account. Between these larvæ and the next stages there are all sorts of intermediate forms, some shorter, some longer, some less and some more mobile, with head and mandibles more or less distinct and active.

Fig. 1 *B* represents a similar intermediate form of the sub-family *Myrmicinæ*. In the sub-family *Formicinæ* the larvæ, although often mobile, are nearly always directly fed by the regurgitation of the contents of the nurses' crop.

But the most extreme condition is seen in *Leptothorax*, in those ants which live by lestobiosis (Part IV) and the sub-family *Dolichoderinæ*, above all in our European genus *Tapinoma*. Here the short, thick larva represented in fig. 1 *C* is entirely stiff and motionless, incapable of eating or even sucking on its own account. Its white, indistinct head shows no perceptible mobility in the mandibles. In short, the larvæ of *Tapinoma* appear to be entirely at the mercy of the regurgitation of the ☿, which accordingly take all the more care of them.

Sometimes, but not always, certain ants, especially our *Lasius*, amuse themselves by selecting their progeny and apportioning them to different chambers—the eggs in one chamber, the larvæ in another, according to size, and the nymphs and cocoons in yet another. Fig. 77 (Part III), taken from André, represents this process very well. But this is by no means the rule, and in general they all lie about the nest at random.

Mild warmth is indispensable to the full development of the ant-brood. Now temperature—especially in the zones wrongly described as temperate—varies enormously, from day to night as well as from one day to another. It varies much more here than in the tropics or the polar regions.

For this reason in Europe, as I had already proved before 1874, the ants that live underground construct *masonry domes*, which enable them to regularize the heat for their brood ; or again they may make use of stones for the same purpose. By day, when the sun is not strong, they take eggs, larvæ and nymphs under the warm roof of the dome or under the stone. By night, or when the weather is very hot and dry, they remove them deep into the earth. In the tropics nothing of this sort is seen, not even in the eastern part of the United States, which are very warm in summer and very cold in winter. But the Niagara Falls, with the fine spray which rises from them and forms a mist over all the immediate neighbourhood, provide an exception to the rule. The domes reappear, as I was able to verify myself while travelling there. So the matter is proved.

I repeat that the anatomical and ontogenetic study of ants has still hardly begun, and that we do not know where and when the differences between the polymorphic individuals ♀, ♂, ☿ and ♃ begin among them. But I will ask those of my readers who persevere as far as Part IV to notice fig. 103, which shows a monster ♀ and a Lilliputian ☿. Here it is evident that differentiation must begin at a very early stage in the larva, if not actually in the egg, which appears to me much more probable ; a hint for the research worker of the future.

We shall presently make the acquaintance of the spinning ants, which use their larvæ as shuttles with which to weave their fabric. Their larvæ have silk-glands considerably better developed than those of the other ants, as we shall see in fig. 133 *B* (Part V), supplied by Wheeler (fig. 133 *A* shows the gland of a species which neither spins nor weaves).

When people referred in the past to complete metamorphoses (transformations) in the Hymenoptera (ants) and incomplete metamorphoses in the Neuroptera (termites), nothing was as yet known of the great transformations which take place in the primitive egg stage of the latter, which we have just mentioned. In my own opinion, the greatest transformation in the ants takes place during their last moult but one, when their larvæ, whose former moults are much less apparent than those of the butterfly caterpillars, turn into nymphs. At this moment the larva either weaves a silken cocoon for itself, in which the change takes place, as in the case of the *Ponerinæ*, or remains naked the whole time, as the *Dolichoderinæ and Myrmicinæ.* In the latter case, it becomes immobile in the forms where it was previously mobile, and then takes on a milky appearance. At last its fine skin splits and underneath appears a nymph, still perfectly white, soft and milky, but already exactly like the adult ant in form, except that all the limbs are folded up and swaddled, so to speak. In the *Formicinæ*, the nymph is sometimes naked (fig. 2 *A*), and sometimes spins itself a cocoon (fig. 2 *B*). In our ash-black ant (*Formica fusca*) we can even see in the same nest some nymphs which remain naked and some which spin cocoons. The nymphs of those *Dorylinæ* with which I am acquainted are all naked.

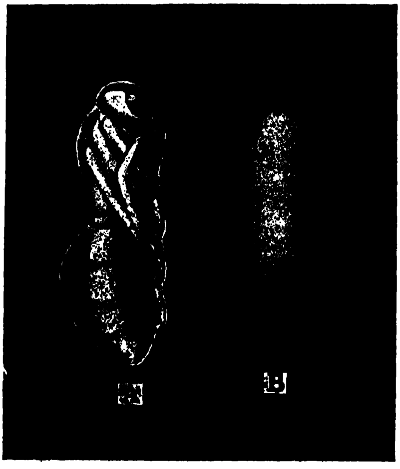


Fig. 2

The metamorphosis, then, is as complete as it can possibly be : but as yet we do not know the anatomy of this transformation, that is, the details of its ontogeny. That is still an undiscovered world, where the body of a larva is transformed in a few days into a body which is ready to become an ant. At first the nymph is white, but although it is without food it becomes stronger and darker every day until it is hatched. Its eyes become black, its body yellow, etc. At the bottom of the cocoon, we may see the remains of excrement and the shrivelled skin of the transformed larva.

Though they do not have to feed them, the ☿ take great care of the nymphs and the cocoons, always transporting them to that part of the nest where the heat is most mild and moist, keeping them scrupulously clean by carefully licking off all dirt, and defending them furiously from attack —just as they do for the eggs and larvæ.

As a rule, those ants which sometimes spin and sometimes do not will spin in the spring and refrain from doing so in the autumn. Gould and Pierre Huber proved that the nymphs of our ants cannot come out of their cocoons alone, and that the ☿ in their nest have to liberate them by stripping the covering with their mandibles. This at least is the case with our *Formicinæ*. On the other hand the nymph of the *Ponerinæ*, which grows more mature, comes out of the cocoon unaided, as I predicted in dealing with *Ponera* and as Wheeler later on confirmed by direct observation in America, in connection with other genera. Pierre Huber had seen that our *Formica* help the larvæ to weave their shell by surrounding them with fragments of earth, which they afterwards remove, carefully cleansing the cocoon once it is finished. He had also seen ants open the cocoons of nymphs which were still young, and had thence erroneously deduced that the naked nymphs of the ash-black ants and others had *always* previously spun cocoons. By enclosing adult larvæ of these species alone in a box in the autumn, shortly before their metamorphosis, I obtained irrefutable proof of the fact that many of them become nymphs unaided, without spinning any trace of a cocoon. This is singular, but it is a fact.

Huber also observed that the ☿ often help the naked nymphs, which are ready for hatching, to rid themselves of their fine, transparent skin and pass into the stage of 'young ants.' He watched them help the emerging ♂ and ♀ to spread their wings. As I felt doubtful about the matter, I conducted some experiments in 1872, although I had already made observations similar to that of Huber. I put into two separate boxes, provided with everything necessary, ☿ and ♂ nymphs of *Tetramorium cæspitum*, which were ready to hatch, leaving the one set alone in their prison and placing with the others in the second box six adult workers. The next day, a ☿ nymph in the first box had already freed herself unaided from her skin, and three ♂ had almost achieved the same result, only the posterior extremity of their wings and abdomen being still entangled in the remains of the pupal skin. I myself freed one of them, and I also took out as they came along the nymphs of the first box, which succeeded in hatching alone during the days which followed. All the ☿ nymphs were able to come out of their skins entirely unaided, but not those of the ♂, which did as the three first had done ; only the one I had liberated obtained normal wings and was free of the pupal skin at the end of its abdomen. In spite of the presence of adult workers in the second box, the same thing happened to the ☿ nymphs.

I then repeated the same experiment with ☿ nymphs of *Formica pratensis*, which were then ready to hatch, and the ♀

nymph of an amazon ant which I had myself extracted most carefully from their cocoons. And every one of them was able to come out of the pupal skin unaided; even the ♀ amazon, which managed on her own account to spread and entirely free her wings and the extremity of the abdomen. As in *T. cæspitum*, the pupal skin splits along the back during hatching. The ant then undergoes regular contortions in order to set herself gradually at liberty, beginning with the head and the thorax, just as most other insects do. The ☿ ant, then, at any rate, is capable of dispensing with the aid of its companions in coming out of the pupal skin.

On another occasion I made a counter-experiment by enclosing in a box, in the same way, ☿, ♀ and ♂ cocoons of many diverse species of the genus *Formica*, shortly before their hatching time. All the nymphs inside perished without being able to hatch, in contradistinction to what took place in the experiment with the *Ponerinæ*. In this respect, then, Pierre Huber was right.

Once more, friend reader, you will note how genuine science teaches us to avoid premature 'generalizations' from particular observations as we would avoid fire! What is true in one place for the one creature is false in another place for the other creature. I would now refer you again to fig. 2, which shows under *A* a swathed nymph in its skin and under *B* an ant cocoon woven out of silk.

A 'young ant' just hatched from the nymph sometimes remains so white and soft that we can hardly distinguish it from the nymph itself. But in the same species it may also sometimes already be darker and tougher.

Everything, therefore, tends to make us believe that nymphs can be hatched at varying degrees of maturity, and that the ☿ which aid them to come out of their cocoon, and even sometimes out of their pupal skin, play no negligible part in the matter, especially when there is any pressing need of assistance. Whatever the case may be, as soon as the young ant is a little stronger, although it may still be almost white, it instinctively begins its social and domestic work in the nest; we shall prove this later on. But it does not leave the nest until later, except under stress of necessity or misfortune. In the first stage of adult ant-life, it learns to distinguish comrades of the same nest from enemies by the aid of its antennæ. And at this point, the ontogeny of ants comes to an end.

POLYMORPHISM

There are several kinds of polymorphism in ants, according to species. In the first place there is *that of the sexes*, which usually, even apart from the sex-organs, differ very widely from one another—in their heads, brains, eyes, limbs, abdomen, etc. as well as their habits. But even at this stage, we must point out certain very important facts of a general character.

1 Unlike the other organs, the digestive tube, particularly the gizzard, of which we shall have more to say, and which differs a great deal according to the group, appears to be always identical, so far as we can tell, in all the sexes of the same species. Yet the ♂ never regurgitates!

2 The fact of having wings entirely transforms the thorax and the eyes in all sexes capable of flying. The eyes become large and prominent; the thorax becomes larger, and is furnished with a special apparatus which is absent or only present in a rudimentary state in those whose dwelling is always on or under the ground. This, as well as powerful muscles, are used in flight.

3 A more or less constant subterranean life brings about an atrophy of the eyes which may amount to total blindness in one sex, whereas the other has enormous eyes. Life in

trees generally improves the sight, but less than the power of flight.

4 Life in the sand or on the steppes brings about (often—not always) a transformation in certain hairs which Santschi called 'psammophores' (sand-carriers) and which are represented in fig. 11 *A* and *B*. Sometimes it also causes the transformation of special individuals called nurses, whose extraordinary swollen crops serve as storehouses of food during the hot and more especially the dry season.

5 As we have already said, heat is favourable to bright colour and variety of form, and cold, on the other hand, to dull colour and monotony of form.

All these five phenomena, and others besides, are instances of what is known as *convergence*, and they are *entirely independent of the true phylogeny* of species. For this reason they all tend to throw our classification of ants, which in itself may and can only be based upon *true phylogeny*, into extreme confusion. I hope that my readers will now realize the importance of the facts I have explained, and will not be satisfied with general terms which only serve to conceal ignorance. They will understand the ontogeny of every polymorphic form, and the reason why the male ant which is deprived of its wings often resembles the worker so closely that they can be mistaken for each other (Plate III, *g* and *h*), that it may even be blind—while others remind us more of flies, or at least of small flying Hymenoptera, than of the ants which we see running about on the ground.

It follows that there is often a special polymorphism proper to each sex among the ants, and always in the case of the female. This we will proceed to analyse more closely.

POLYMORPHISM OF THE ♀. There are species and even whole genera in which the normal ♀ is born and lives permanently without wings, but in the vast majority of cases she is winged, and her thorax, in consequence, is powerfully formed. As a rule, she is the largest individual of the community. She, or rather they—for there are often several in the same formicary—are the mothers of all the rest. Often, though not always, they are surrounded by a court of workers, which feed and protect them and gather up the eggs they lay, egg-laying being their special rôle.

But the most regular caste derived from the ♀ is the worker (☿). It is only in certain species whose social life has degenerated into complete *collective parasitism* that the worker has gradually disappeared. In the first chapter we saw the first stage of such a disappearance in connection with *Strongylognathus testaceus* (fig. 104 of Part IV), as well as with *Anergates atratulus*, in which it is complete. Social parasitism has here rendered the worker useless. In other species known as the slave-makers, she is transformed and becomes a pillager (Plate III) instead of remaining a worker.

Here again we see intermediate semi-predatory, semi-worker forms, which demonstrate for the phylogeny of slave-making.

But the worker herself often shows a more or less complete polymorphism, with transitions. Whereas in many species all the ☿ are alike and about the same size, *e.g.*, species a, b and c in our first coloured plate (Plate I), there are other species, such as *Formica pratensis*, for example, often pictured in Part IV (*e.g.*, Plates X and XII), in which the size varies ; in these, the head of the little ☿ is proportionately larger. This disproportion may gradually extend so far that we come to the extreme case pictured in Plate III (*Pheidologeton diversus*) : the large ☿ *a*, the medium-sized *b*, and the small *c*. And furthermore, all the transitions between *a* and *b* and *b* and *c* are present ! What does this mean ? The study of habits gives us our answer.

Pl. I.[1]

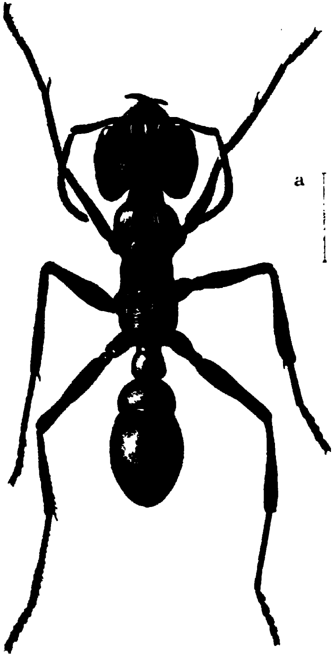
a. *Myrmecia aberrans* For. ☿. 14·5 mm.

b. *Myrmecia* (*Pristomyrmecia*) *mandibularis* Sm. r. *aureorufa* For. ☿ 15 mm.

c. *Phyracaces singularis* For. ☿. 6·8 mm.

Part. i.

Pl. I.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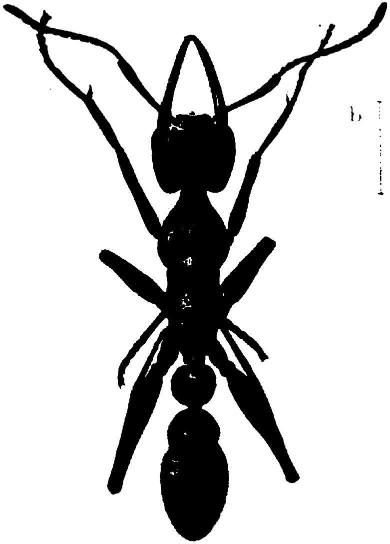
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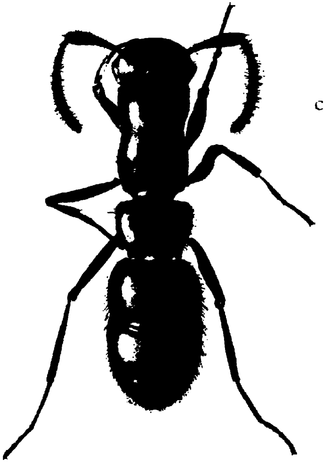
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INSTITUT POLYGRAPHIQUE S.A. ZURICH

E. W. Heinrich del. et col.

Almost invariably, the little ☿ is occupied in work inside the nest, and in its external defence and the search for food. The big ☿ herself is differentiated in the first place for certain work which demands more strength, and also partly for defence. But phylogeny teaches us that it is the large one which, especially in the conformation of the head, bears most resemblance to the ♀. At the same time, there are exceptions, as we shall see.

Apart from this, the big ☿ adapts herself, little by little, to special occupations which differentiate her more and more. Thus that of *Pheidologeton* (Plate III), of *Messor*, etc., grinds up seeds and cuts other kinds of solid food (insects or flesh) into small pieces, as Oswald Heer proved so long ago as 1852 in his *Hausameise Madeiras*. Again, as we see in Plate III, the large ☿ of *Pheidologeton* carries her little sisters on her great head when the colony moves into another nest. Jacobson and others noticed this, and submitted it to proof. We have only pictured three, but a large ☿ can carry as many as twenty little sisters, crowded upon her broad head.

On other occasions the big ☿ is adapted to guarding the entrance of the nest with her large head, and thus driving away any thieves or enemies which attempt to find their way in. In this case, we observe a gradual phylogenetic tendency for the head to become more and more obtuse in front. Then the anterior surface (front) begins to form a more or less marked curve which separates it to some extent from the upper surface of the posterior portion of the head (vertex and occiput). That is the origin of a matter which we shall discuss when we come to the porter ♃ (Part V, fig. 135 and 136).

In yet other cases, the large ☿ gradually acquires by phylogeny, as we see especially in certain *Ecitons*, longer and longer mandibles or pincers, which are pointed or crooked (fig. 3 *B*). These are no doubt used in defending the nest against the mammalian *myrmecophagi* (ant eaters) such as the pangolin and scaly ant-eater, by biting their tongues and skin ; thus phylogeny gradually forms in various genera of ants the creature known as the 'soldier' (♃). The term is very unsuitable, for it is the worker, even the little one, which is for most of the time the real defender of the nest. The ♃ is simply formed in phylogeny by the gradual disappearance of the medium-sized ☿, as the small and large ☿ become more and more different from each other. Thus in the large genus *Pheidole* there are no medium-sized workers left, except in a few sub-genera. In the sub-genus *Machæromyrma* of the genus *Cataglyphis* (Plate I *h*, *i*, Part V), the medium-sized ☿ are rare, and in the genus *Eciton* they are still abundant.

Hence ♃ is only used when the medium-sized ☿ have almost entirely disappeared, or again where the peculiarities of the large ☿ are so special that they demand an *ad hoc* designation as in the case of the ♃ of the *Ecitons* (fig. 3 *B*). Thus we see that it is idle to wrangle about the terms ☿ and ♃. The soldier is only a large worker, particularly well differentiated from the small ones, in view of a special function.

And so we gradually reach the porter ♃ of *Colobopsis*, whose head is entirely truncated as though with a razor. (Plate XIV *f.g.*, Part V) the *Pheidole* ♃ whose head is larger than its body, and other similar peculiarities. But where there is no ♃; we sometimes see the opposite peculiarity, that is to say the worker is extremely small, absolutely *monomorphic* (having only one form) and quite different from her enormous ♀. Here we are obliged to agree with Emery that their species must have possessed polymorphic ancestors with a ♃ and a very large ☿. This is the case, for example, with the genus *Carebara*, whose species *vidua*, in the natural proportions of the worker relative to the ♀, is represented in fig. 103 (Part IV). A similar extreme is due to the murderous parasitism which I have called *lestobiosis*, and with which I will deal later, in fact *Oligomyrmex*, a relation of *Carebara*, often has a ♃ with a horn at each extremity of its head and lives in lestobiosis.

But there are yet other forms of polymorphism in the ♀ of the ants.

In the first place we must mention *microgyny* (smallness of the ♀). We sometimes see among our ants, our ordinary red ant (*Myrmica rubra*) for example, certain ♀ which are much smaller than the others. The thorax is proportionately narrower than that of the large ones, and they seem to be less fertile. For the rest, they have wings and are like other ♀. In certain species of *Leptothorax*, *e.g.*, our *acervorum*, which lives in tiny nests under the bark of trees, the ♀ is normally scarcely any larger than the worker. This is probably owing to the fact that she has few eggs to lay, on account of the minuteness of each nest and the short duration of its existence; in spite of this, we not infrequently find several ♀ there.

But there is another kind of microgyny which is due to the parasitism of the ♀. Instead of rearing her brood herself, she compels a colony of another species to adopt her, either by attaching herself to the fertilized ♀, or by assassinating her, or in some other fashion. This happens for example in certain *Formica* and the exotic sub-genus *Oxygyne* of the genus *Cremastogaster*. The ♀ of the Oxygyne has also, like that of *Strongylognathus* and *Polyergus*, arched and pointed mandibles without teeth. This made me think that the Oxygynes could easily thrust their mandibles into the head of the ♀ of the working species, among which they live cuckoo-fashion, for their ☿ have mandibles well-provided with teeth.

But there I go again! With these hypotheses we are in danger of talking nonsense, and we must reserve our judgment until we have experimental proof. Such microgynes are sometimes smaller than their ☿, for example in *Formica difficilis* and *microgyna* of the United States.

Another form of polymorphism in the ♀ gives us the *ergatogynes*, which means 'females in worker form.' These are not parasites; they are wingless females with a thorax entirely or almost entirely like that of the ☿, but a fairly strong body and above all a large abdomen with well-developed ovaries. Two possibilities present themselves here:

The ergatogyne may exist side by side with the ordinary winged ♀, as in Huber's amazon ant (*Polyergus rufescens*) pictured in Plate III *l*. I beg the reader to compare her with the winged ♀ *m*, the worker *n* and the ♂ *k*, which is black, whereas the three derived from the ♀ are red. This 'apterous female,' already observed by Pierre Huber, may replace the fertile winged ♀ if the latter should chance to die. I have myself found, and have more especially received, from foreign countries, similar ergatogynes belonging to various genera of ants and their various species.

Why did they appear in the phylogenetic process? For some reason which still eludes us the normal winged ♀ may not have fully sufficed, and the gradual development of aberrations like these may have been advantageous in prolonging the life of the colony.

Or it may be that the normal winged ♀ entirely disappeared in the course of phylogeny, and the ergatogyne alone was left, as in the case of the large genus *Leptogenys*, with all its sub-genera, and probably also of the genus *Diacamma*. These genera have a winged ♂, but there was much vain search for 'Madame Lobopelta' as she was called by my friend Wroughton in India, who eventually was the first to discover her in the heart of a large colony. I will refer the reader to the same Plate III, figs. *d* and *e*, which represents the worker and ergatogyne of a *Leptogenys* of the sub-genus *Lobopelta*. Here the ergatogyne is a little more distinct from the worker than in the one discovered by Wroughton, which is scarcely distinguishable except by means of her large abdomen. In these genera, therefore, the ergatogyne has entirely replaced the ♀, and thus there arises a problem of phylogeny for those who love hypotheses; have the ergatogynes been directly produced by a continuous regression from the winged ♀, which accordingly became useless and disappeared? I leave it to the quibblers to reply to this by some long theoretical disquisition. Here we have something better to do, so we will say no more.

We must not confuse the ergatogynes with the wingless and often blind females of the large sub-family of the *Dorylinæ*. Yet a problem arises here which is similar to the preceding one. Can the ♀ of the direct ancestors of *Dorylinæ* have had wings which have been lost, or did they never have them, like the Mutillids? For my part I incline towards the first hypothesis, though I cannot prove it; The ♀ of the *Dorylinæ* are very large and entirely different from the ☿ (as can be seen in fig. 107, *A*, *B*, *C*, *D* and *E*, Part V). Their whole bodies differ almost as much from those of the worker as from those of the ♂, so much so that the old writers placed the same species of *Dorylinæ* in three different genera. Here again, we must learn to avoid hypotheses concerning phylogeny.

POLYMORPHISM OF THE ♂. In the ♂ the matter is simpler than in the ♀. Briefly, there are only two kinds of ♂: the ordinary normal winged male and an apterous male, which generally resembles a ☿ so closely that they can be mistaken for each other. If the reader will look at Plate III and compare the ♂ *h* and its ☿ *i*, he will see that I am right. Sometimes, even, this ♂ is totally blind, and it is practically the genital organs alone which serve to distinguish it. Again, there are species, especially in the genus *Cardiocondyla*, in which the ♂, which still lives underground, is pale and more or less yellowish, whereas its ☿ is black.

Here also there are two sorts of transitions. Although in certain species the ♂ is always apterous, in others a winged ♂ exists at the same time. This is the case for example with *Ponera Eduardi*, the winged ♂ of which is represented in Plate III by the letter *f*, and the wingless ♂, which closely resembles its ☿, by the letter *g*. Here we should be faced with the same problem of phylogenetic origin as in the case of the ♀, if it were not evident that every wingless ♂ comes from winged ancestors. Greater or less fertility is not here in question as with the ergatogyne, and among the male ant-folk no one ever works at any other business except mating: there are no 'worker' males.

Another transition may be seen in *Anergates atratulus*, represented in my work on the Ants of Switzerland, whose ♂ is apterous although its thorax is analogous to that of a winged ♂. The nymph still possesses rudimentary wings with their articulations, but these vestiges disappear at the time of emergence. Hence it is evident that the ancestors of *Anergates* had a winged ♂, and it seems to me certain that the ♂ of this ant provides the key to the origin of the apterous ♂.

One fact which has hitherto appeared to have no exception is that in all the ant species whose ♂ is apterous, the ♀ is *always* winged, and that conversely in all those whose ♀ is wingless the ♂ is *always* winged. No species is known in which both sexes are apterous.

Another fact is that whenever the ♀ is winged and the ♂ apterous, the former shows no signs of her usual coyness, which consists in a pretence of trying to escape from the male. On the contrary, it is rather she herself who seeks the union.

Here a serious question arises. When the virgin ♀ are apterous they generally go out at night in groups from their own home, and winged ♂ come from other colonies to mate with them, so that crossings are effected, almost in the same way as in the nuptial flight of most ants. But what happens when the ♂, which is always wingless—as in the case of *Cardiocondyla Stambuloffi*, for example, whose male is yellowish in colour, or again in *Anergates atratulus*—does not leave the nest, and its inhabitants are all born from a single mother? This certainly applies to *Anergates*, whose colonies, moreover, are far apart, restricted to one nest, and rare. I myself, like von Hagens, have contrived to observe at my ease their union in colonies with artificial and natural nests. The ♂, as slow as he is clumsy, approaches his little winged ♀, who herself helps him to settle upon her. This takes place *inside* the nest, or at any rate at its entrance. Only afterwards do they take wing and fly away to found new parasitic colonies, each on her own account.

Logically it follows that at any rate in *Anergates*, whose colonies never have more than one fertilized mother, and probably in many species with ♂ which are always apterous, every ♀ *can only be fertilized by one of her own brothers, born of the same mother!* I have described this sort of marriage as *perpetually consanguine* '*adelphogamy*' (marriage between brothers and sisters). Now this fact, which at present seems to be unique in nature, appears to be in flagrant contradiction with what we found out at the beginning of this chapter in connection with parthenogenesis, about the apparent necessity for a certain cross-fertilization, even for microbes, at least between the nuclei of different cells. In adelphogamy there is certainly an exchange of cell-nuclei, but only of cells which have the direct relationship of sisters to each other. Here, therefore, a question arises : why does not the ♀ *Anergates* reproduce herself simply by perpetual parthenogenesis, since her constant adelphogamy *appears* to amount to the same thing by concentrated and lasting consanguinity? Yet, far from being parthenogenetic, this ant has numerous great hulking men-folk, even larger than their little flying, if not flighty, wives !

Now nature is not in the habit of conserving for very long creatures which have become useless: we have seen this in connection with the parasitic ants, from which the worker has disappeared—as in the example of *Anergates*—or from which she is about to disappear, as in *Strongylognathus testaceus*. Why then does this big male fellow flourish so merrily in *Anergates atratulus ?* It must be that his spermatozoa have some use. Adelphogamy cannot therefore be the exact equivalent of parthenogenesis. We must be content here to ask the question, and leave to the future the task of answering it with the aid of new observations.

In *Formicoxenus nitidulus*, which also has none but apterous ♂, R. Stumper has recently proved the existence of numerous different little colonies in a single large nest belonging to its hosts, *Formica rufa* and *pratensis*. Here, then, it is possible that the ♂, which are more active than those of *Anergates*, are sometimes mated, although they have no wings, with ♀ from other colonies. In *Cardiocondyla*, on the other hand, in which only one known species has winged ♂, constant adelphogamy appears to be the rule with the other species, since they live in the sand in small separate colonies at a fair distance from one another.

Chapter III

EXTERNAL ANATOMY

The external and internal anatomy of ants is a miniature of our own. The cells, the elements of all life, are not on an average any larger in their case than in ours; part of an organ, however complicated it may be, is therefore composed of only a small number of cells. It follows that there is a limit of smallness which insects with such complicated habits as the ants cannot exceed, if every part of an organ is to account for at least a few cells. We shall find some curious things in this connection when we come to the internal anatomy. The fact is, we know of no ants measuring less than 0·8 mm. in length. That is the extreme limit, below which no ant can exist. On the other hand, the largest known ant, the ♀ of *Dorylus* (*Anomma*) *Wilwerthi* attains to more than 4 centimetres in length (42 mm. It is depicted in Part V, fig. 107 *B*).

Not only the size but also the form of the ant is extremely variable, as will be seen in Plates I to III and in fig. 3, as well as in the other Plates in these volumes. Certain ants of the genus *Echinopla* are almost round, and are covered with bristles like hedgehogs; others are long and narrow like threads ; others again are flat ; their different organs vary infinitely.

I therefore beg you, dear reader, not to grow impatient if I give you here a detailed description of each part of the bodies of my little friends. As we proceed, I will tell you what their various organs are used for. Remembering what we have said as to their phylogeny and ontogeny you will understand the vast number of different functions and purposes to which the 7,500 species, races and varieties of ants are adapted. And do not forget their polymorphism, which often makes the number of divergencies three or four times as large!

We will divide the external anatomy of the ants into five parts: 1 The Head; 2 The Thorax; 3 The Peduncle or Pedicel; 4 The Abdomen; 5 Sculpture, Hair, Pubescence and Colour.

1 Head

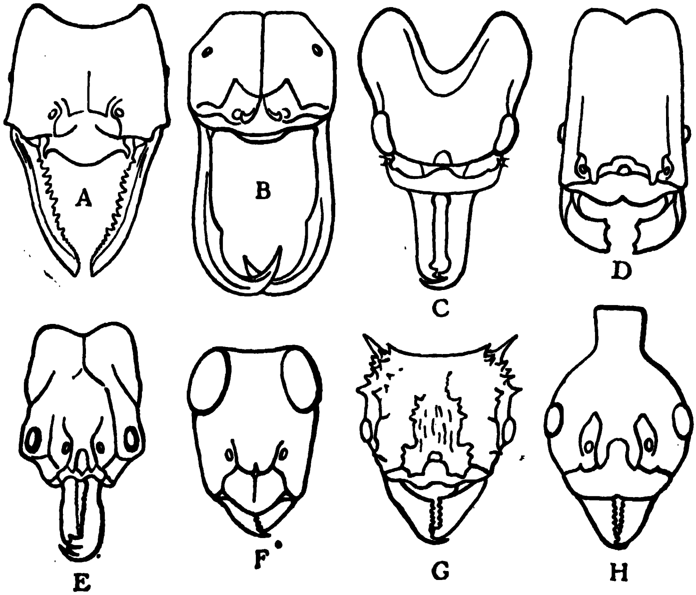


Fig. 3

The head itself has infinitely varied forms and eight different foreign types of these are shown in fig. 3 *A* to *H*, all unlike that of our ordinary European ants. The regular head-form of these last is represented in fig. 6; we will take it as a model, which can be compared later with those of other forms. Certain ants have flat heads ; an extreme form of this kind will be represented in fig. 30 (Part II). Certain ♃ have enormous heads, like that in Plate III *a*.

MANDIBLES. Ants use their mandibles for almost everything: biting, pricking, piercing, cutting off heads, building, sawing, gnawing, cutting, carrying, leaping and even bounding, but never for eating. Letter *H*, fig. 6, represents the ordinary, or we might say normal, form of mandible. It is roughly triangular and twisted at the base. It has three edges: 1 an external convex edge; 2 an internal edge which is more or less concave, not only lengthways but also breadthways, especially near the base; 3 a toothed edge which I have called a 'terminal edge,' used in biting, carrying and sawing. The base of the normal mandibles (fig. 3 *G*) is strongly articulated on each side at the extremity of the anterior edge of the head, and is moved by a strong muscle (fig. 28) of which we shall speak later. The number and size of the denticles vary enormously, generally from two to eight or nine, but often more. The last denticle is generally longer and forms the point. Those which lie near the inner edge are often indistinct. In the ♂ the denticles are often entirely absent: there are even certain ♂ ants whose mandibles are so atrophied that they do not meet in the middle. The normal mandibles are comparatively thick, long, curved, etc., according to the species and their use. In ants which gnaw wood they are thick and short, but especially in granivorous ants, in which the denticles are eventually quite worn away by grinding the grain, as we see in fig. *a*, in Plate III, and in fig. 3 *D*.

In the leaf-cutting ants, *Atta*, etc. (fig. 3 *G*, and in Part V, fig. 114 *A* and *B*) the mandibles often have no denticles, at least in the large and medium-sized ☿; they are sharp and serve to cut leaves and the skin of enemies which attack their nest. I learned this fact from personal experience in Colombia, where they drew blood.

In the *Odontomachini*, the long, narrow mandibles inserted in the middle of the head, as we see in fig. 3 *E*, have two parallel edges and generally only two or three sharp teeth arranged vertically one upon the other at the terminal edge. These insects do not leap, as has been supposed. When an enemy approaches, they open their mandibles to their utmost extent. If a finger is held out to them, they make as though to bite, thrusting the body forward and at the same time closing their two pincers so as to force the whole body backwards, with the aid of the jerk thus given, and do not actually bite. This backward spring may cover several inches. I have myself confirmed the fact in the Antilles and Colombia. At the same time, in the large *Odontomachus* at any rate, the violent closing of the mandibles is perceptible to the ear as a sharp little sound which has caused the Indians and Creoles of Colombia to name this insect the 'Tak ant.' The mandibles of *Myrmoteras* (Plate VIII, *c* in Part III) are similar to those of *Odontomachus*.

The *Dacetini* have a triangular head, usually flattened, broad behind and narrow in front, and mandibles which are often similar to those of *Odontomachus*, but also often provided with long teeth on the inner edge. It can be seen in fig. 3 *C*, as well as in the Plate XVI, Part V (*Orectognathus*).

We have already pointed out in Chapter II, in connection with the polymorphism of the ♀, the probable use to which the ♃ of some species of *Eciton* put their long, narrow, curved and pointed mandibles, depicted in fig. 3 *B*. It is the same with *Machæromyrma* pictured in Plate XIV *h.i.*

in Part V, although the form of their mandibles is very different.

We have already spoken in our second chapter of the curved and pointed mandibles of the amazon ants and *Strongylognathus*, which serve to pierce the brains of their enemies, and which are pictured in Plate III (and in figs. 104 and 106, Part IV). Other species besides these have similar mandibles, though their purpose is as yet unknown; *e.g.*, true *Leptogenys*, the termite-eaters, whose mandibles are articulated a considerable distance from one another at the two anterior corners of the head, and very slender, so that even when the tips are joined there is an immense empty space between them.

The most curious mandibles are undoubtedly the double ones which have two uses. Those of the genus *Acanthognathus*, which moreover resemble those of *Orectognathus* (Plate XVI, Part V), and are very long and narrow, bear at about a sixth of the distance along their inner edge a second, superimposed pair of mandibles. These are shorter, turned obliquely back, and themselves furnished with distinct denticles. When the long mandibles are closed, the small ones are completely crossed. But when the large ones are open at the ends, so as to form a right angle with the longitudinal axis of the body, the small ones function on their own account, and their denticles meet. Dr. Möller has proved that it is by means of these small mandibles that *Acanthognathus* lifts up and carries away its eggs, larvæ, etc., as well as the earth with which it builds. But as soon as someone scares it or pinches one of its legs, it closes its big mandibles in order to bite, probably in the manner of *Odontomachus*.

The strangest of them all are the mandibles of the genus *Harpegnathus*, depicted in Plate XIV, *K* (Part V). This

Indian genus, observed by Wroughton, takes alarming leaps of more than a yard, with the aid of its long mandibles, which have a slight upward curve. The entire head bends underneath the body, and then stretches out in front, somewhat in the manner of the thorax of our European insect called the click-beetle. Near the base of its large mandibles, *Harpegnathus* bears a very powerful triangular tooth with a downward slant, and this tooth is itself partially denticulate in front. I am of the opinion that this tooth may serve as a second mandible for carrying the brood and for building in the manner of *Acanthognathus*, but with this difference, that it can only do so when the large mandibles are half-open. These mandibles grow narrower towards their ends, where they only have denticles.

While on the subject of curious mandibles, I must also mention those of *Mystrium*, pictured in fig. 3 *A* (and Plate XVI, Part V), as well as those of *Emeryella*, from the island of Haiti, which are similar. I may also refer to the singular mandibles of *Anomma*, pictured in fig. 107, *C*, *D*, *E* (Part V), as well as those of the genus *Belonopelta*, which are narrow and long, with immense spines on their inner edge.

Lastly, there is the genus *Myrmecia*. The mandibles of two of its sub-genera are shown in Plate I *a* and *b*. Those of *Myrmecia Mjöbergi* are much longer and narrower even than in the case of *aberrans* represented in fig. 2, of Plate I, and have as many as 26 teeth on their enormous terminal edge. In *Pristomyrmecia* this edge is absent, and is replaced by an internal edge (fig. *b*). The genus *Stigmatomma* has mandibles similar to those of *Myrmecia*, but they often possess two longitudinal rows of teeth, one above the other.

In the ♂ most of the singular forms of mandibles we have described are replaced by the ordinary and relatively atrophied form mentioned above.

JAWS, LIPS, TONGUE, AND FEELERS. Ants suck and lick, but they do not chew, and their tasting apparatus is formed accordingly. It is hidden under the normal mandibles when they are closed, and thus they cannot be seen in fig. 6. When an ant is eating, it thrusts out its tasting apparatus with the aid of the complicated muscles of the pharynx which set the whole apparatus moving and save the ant from the necessity of opening its mandibles. I would ask the reader to examine carefully figs. 4 α, β, γ.

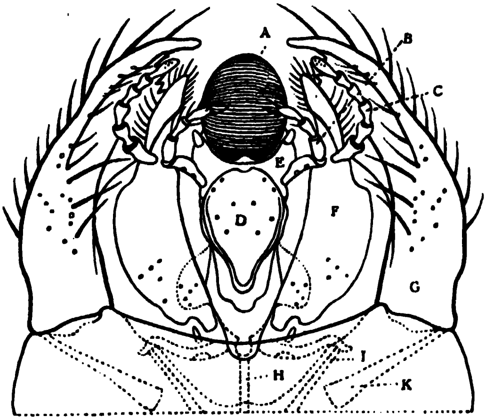


Fig. 4 α

In figure α (head of *Myrmica* seen from beneath), the muscles known as *abductors*, which *open* the mandibles (*G*) are indicated, as at *K*, by dotted lines. Similarly, the *adductor* muscles, which *close* the mandibles (*G*) are indicated as *I*, but only their terminations are seen there, for they continue, and broaden, as far as the chitinous skin at the back of the head, as is shown in fig. 28. It is these muscles which give the mandibles their tremendous strength, in the granivorous and leaf-cutting ants, for example. Letter *F* (fig. 4 α) shows the jaw with its maxillary feelers of six segments, distinguished by the letter *C*. The mobile tongue, transversely ridged, is denoted by the letter *A*, and in fig. 28 we see this same tongue with the long narrow muscles which move it. Fig. 5 shows the tongue (letter *b*) in profile. Letter *D*, fig. 4 α, shows the lower lip, which adheres to the chin and encloses the opening of the large salivary gland of the thorax, this *exit* being represented in fig. 5, *a*. X in this same fig. 5 shows the continuation of the duct, and *G* the gland itself. On the other hand, *B* in fig. 4 α, shows one of the two palpi known as *labial*, each of which consists of four segments.

Figure 4 β represents the jaw alone, without its palpus, in order to show the very fine comb (*M*) which it bears, with minute gustatory organs like little dots at the base. *S* indicates the base of the jaw.

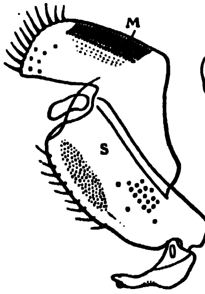


Fig. 4β

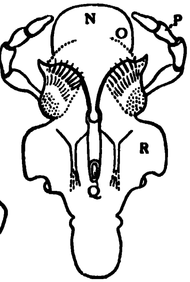


Fig. 4γ

Its rounded extremity, on which we find the comb, terminates in a row of hairs.

N in Fig. 4 γ shows the tongue without its wrinkles, but with gustatory organs *O* at its base, the salivary duct *Q* (section) and the lower lip *R*, not to mention the labial palpus *P*, already indicated in fig. α.

The number of articulations in the maxillary palpi varies from one to six, according to the species, and that of the labial palpi between one and four. Besides the comb attached to the jaws (fig. 4 β *M*), there is another comb, or brush, with longer and stronger hairs, on either side of the base of the tongue (known as the *paraglossa*). These combs play an important rôle in the fastidious toilet-attentions which the ants bestow so lavishly upon their companions, larvæ and

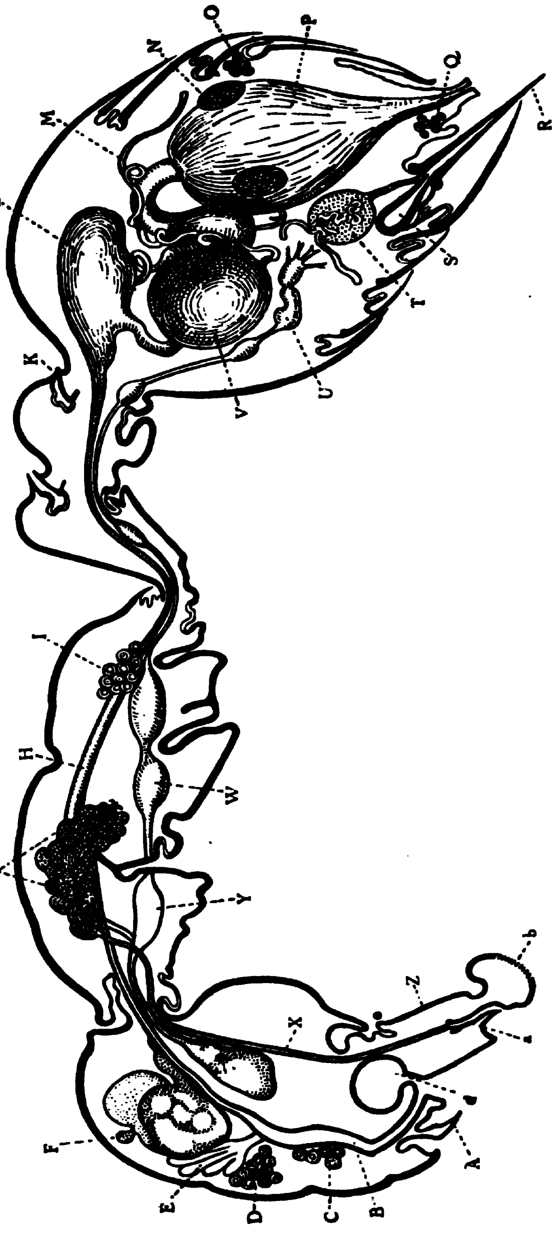


Fig. 5

nymphs. The tongue itself plays the most important part in licking, but its combs help it to get rid of the dirt.

Behind the paraglossæ (which wasps, but not ants, use for chewing) is the throat, and behind that a rounded sac always full of the débris of food—the 'buccal sac,' seen in profile in fig. 5 *d* ; this is a very interesting organ of which we shall speak later ; in general, it appears to be chiefly a reservoir for waste matter.

The mouth and the entry to the pharynx (fig. 5 *B*), where the œsophagus (fig. 5 *H*) begins, are covered by the upper lip or labrum (fig. 5 *A*), which is mobile from top to bottom, closely applied to the chin, and hidden under the closed mandibles and the epistoma, though it opens when the ant is eating.

You will think this an alarming list of complications, dear reader, for such insignificant little creatures ! But I entreat you to be patient: a little effort of attention will help you to understand the fascinating social habits of the ants by reason of their anatomy. Pray, then, have courage.

DORSAL ASPECT OF THE HEAD. *Epistoma* (clypeus), fig. 6 *G*. Situated immediately behind the mandibles, this mobile piece, edged with sutures, varies greatly in form according to the species. A glance at the various heads *A* to *H*, fig. 3, and those of Plates I to III, will suffice to make this clear.

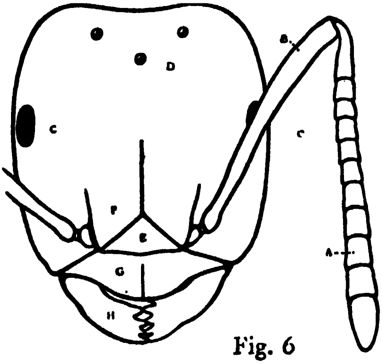


Fig. 6

Frontal area ; fig. 6 *E*. This is a small triangle, often rounded at the back, though often lacking.

Frontal groove. This is the groove which extends the posterior angle of the frontal area backwards over the middle of the head. It too is often absent.

Frontal carinæ. On each side of the frontal groove is a ridge which is usually sinuous but sometimes straight, and which may also be absent. The two frontal ridges can be very near to each other or wide apart, according to whether they extend to the eyes and the edge of the head, as in *Daceton* (fig. 3 *C*) or even beyond the edge of the head, entirely covering the eyes, as in *Cryptocerus.* In *Cr. clypeatus* ♀ and ☿ (Plate XIV *b.c.* in Part V) they are translucent, and cover the eyes. In *Cr. varians* ♀ and ♃ (Part V, fig. 138 *B. C.* in Part V) they even *encircle* the head, which they cover like a bowl, entirely hiding the eyes, antennæ and mandibles. The frontal carinæ vary, therefore, to a remarkable extent, even for the sexes of one species, as will be seen in the ♂ in *a* and *A* of the figures of the two species just mentioned. This also is an interesting fact of phylogeny.

Front, fig. 6 *F.* Situated between the frontal furrow and the frontal ridges, the front varies according to these last in form and size, as we see in the heads in fig. 3 and others.

Cheeks. This name is given to the part of the head situated between the frontal ridges, the clypeus and the edge of the head. Thus in *Cryptocerus*, *Daceton*, etc., the cheeks are hidden in front and lateral to, or even under, the frontal ridges.

Compound eyes. Fig. 6 *C.* Situated on each side, the compound eyes may have a number of facets ranging from zero to a thousand (and even more in the ♂ *Dorylus*). They may be placed well to the front (fig. 3 *E*) or right behind (fig. 3 *F*) or even hidden under the frontal ridges, as in *Cryptocerus*, which see and move sideways. Certain ants are totally blind.

Ocelli; fig. 6 *D.* The three simple eyes or ocelli are arranged in a triangle, separating the front from the vertex. Two of them are paired, and situated behind; the third, which lies in front, is unpaired. As a rule though not always, they are a little larger than a facet of the compound eyes, and they are often entirely absent, especially in the ☿ and ♃. Sometimes the anterior ocellus exists alone.

Vertex. Situated behind the forehead, the vertex is very ill-defined and passes imperceptibly to:

The *occiput* or back of the head, which is joined to the thorax by a more or less mobile articulation. Often there is a posterior edge to the head, forming an abrupt curve or even an angle between the vertex and the occiput proper. But sometimes the head forms a more or less distinct neck behind the occiput, as in fig. 3 *H* and Plate II *c*. In other cases the head has spines (fig. 3 *G*) or horns, teeth, angles, etc. In short, we should never finish if we tried to describe it all. In Plate XIII, fig. *d* (Part IV), we shall even see an ant with spherical eyes set on rods!

Between the frontal carinæ, the cheeks and the epistoma we observe (fig. 6) a socket, at the bottom of which the antennæ are articulated; it is called a clypeal socket. Sometimes the antennæ are articulated higher up, towards the middle of the frontal carinæ, as in the genera *Camponotus* and *Polyrhachis*; we then speak of an antennary socket separate from the clypeal socket.

ANTENNÆ: fig. 6 *B.A.* The extremely mobile articulation of the antennæ is spherical, like that of our arm on the shoulder. It is continued in an elongated joint called the *scape* (fig. 6 *B*), which is generally straight and rarely curved, bent or flattened. At its extremity, the scape is jointed with an elbow (mobile only in front), to the *funicle* (whip) of the antennæ; fig. 26 *A*. But this funicle, which consists of from 3 to 12 joints in the ☿ and ♀ (as many as 13 in the ♂), is on this account very mobile. Here is located the sense of smell, which I have called *topochemical.* It is often more or less swollen into a club at the extremity, and it is this mobile club which contains the nerves of smell.

VENTRAL ASPECT OF THE HEAD. The lower anterior part of the head is represented in fig. 4 α; there we see the mouth parts, especially when the mouth is thrust forward and open, ready to eat, and I shall not mention it again as I have described it above. Behind this, starting from letter *H* (fig. 4 α) is a deep longitudinal suture which divides the under part of the head into two halves and is bifurcated behind before it reaches the articulation of the head and thorax. This articulation contains the occipital opening, which provides a passage to the œsophagus, the nerve-chain and the salivary duct; it can be seen in fig. 5. Apart from this the ventral part of the head, beyond which stretch the long maxillary palps found in certain species, has no particular interest, except it be for the psammophores or macrochætes (fig. 11) of species living in the sand.

2 THORAX

Situated between the head and the pedicel, the ant's thorax consists of four parts: the prothorax, mesothorax, metathorax and epinotum, parts which vary enormously according to whether the ant is winged or not. Each of the first three is composed of a dorsal portion or *notum* and a ventral portion or *sternum* which bears the legs. Very often the sutures or deep lines of the demarcation between the various parts of the thorax are partially or wholly lacking. The thorax is often furnished with spines, in front, behind, and even in the middle, as we see in Plate II, fig. *c* and *a*, but even better in Plate XVI (*Orectognathus*), Part V. The thorax may be contracted, flattened, edged, provided with various appendages (Plate XIV, *b* and *c*, Part V), even spherical or almost so (in *Echinopla*), and sometimes, on the other hand, very narrow and elongated, as in Plate II *c*.

The *wings* and *legs* of ants are appendages of the thorax.

PRONOTUM. The pronotum constitutes the back of the *anterior thorax*. Look at the picture of the beautiful ant *Myrmecia aberrans*, in Plate I *a*. Behind the head we see the red pronotum furrowed with longitudinal striæ, which diverge behind. Behind this is a deep transverse suture, which separates it from the mesonotum, that is, the part adjoining the pro-thorax. In fig. 5, on the other hand, the pronotum and mesonotum combined form a single hollow behind the head, the suture being almost obliterated. But here we may see in profile between the mesonotum and the adjoining part a cavity which corresponds to a suture. The ☿ ants *a* and *c* in Plate III, bear a spine on the front of the pronotum. This is very common.

In the winged ♀ and ♂ the pronotum is thrust from the back to the front by the mesonotum, which frequently overhangs it to such an extent as to hide it.

PROSTERNUM. The prosternum can only be seen from beneath. But it alone is articulated with the head: the pronotum merely covers the articulation. The prosternum consists of a single plate which, viewed from below, is roughly triangular, the base of the triangle being behind. The anterior coxæ are jointed in front to the prosternum and behind to the trochanter.

MESONOTUM. In the wingless sexes, it is the middle part of the thorax which often forms one piece with the pronotum. It adjoins the pronotum, and is coloured dark in the ant shown in Plate I *a*. But seen from the side (*e.g.*, figures *g* and *h*, of Plate IV in Part II) the mesonotum of the worker and ♃ is continued underneath in a lateral part of the mesonotum called the *scapula*. In the winged sexes, owing to the strong muscles of the wings, the mesonotum is transformed into a raised disc which thrusts the pronotum in front and the metanotum behind. These sexes often have longitudinal or convergent furrows, and near the middle of their sides the two pairs of wings are articulated, as we see in figures *k* and *m* of Plate III. Behind the mesonotum there appears first of all an appendage, which is more or less transverse and very narrow, in the middle (or even replaced by a simple suture), an appendage called the *proscutellum*, and behind this a disc rounded behind and truncated in front, called a shield or scutellum. These two organs, which can be seen in the same figures *k* and *m* of Plate III, between the wings, are separated from each other as well as from the metanotum by the sutures of the mesonotum proper. On the sides of the mesonotum of the winged sexes are four or five lateral pieces, according to the species, situated under the wings (*epimera* and *episterna*) which stretch from the mesonotum to the mesosternum.

MESOSTERNUM. Apart from the episterna of the winged sexes, which appear at the base of the sides of the thorax, behind the epimera, and apart from the lateral scapula of ♀ and ♃, as well as those of the wingless ♀ and ♂, the lower part of the mesosternum possesses only a flat square lamella, to which the coxæ of the middle legs are articulated on either side, as those of the anterior legs are articulated to the prosternum.

METANOTUM. Long confused with the epinotum, the true metanotum of the ants is an atrophied organ, as Emery and Janet have proved. As a rule it forms between the mesonotum and epinotum a simple hollow provided with two stigmata or respiratory openings, slightly raised, as in Plate I *a*. At the side it grows broader towards the scapula, which appears like two triangles in the same figure. But in certain species it is raised and broadened into a transverse dorsal rectangle, thus forming an intermediate piece between the mesonotum and epinotum, as in the case of *Plagiolepis*, for example. It is almost the same in the case of the winged sexes, where it was formerly called *postscutellum*, because it came after the shield.

METASTERNUM. Laterally, this consists in the broadening of the *scapula*, and for the winged sexes, in the aforementioned episterna. Underneath, where the coxæ of the hind legs are articulated, it is identical with the mesosternum. But behind, conjointly with the epinotum, with which it is fused, it is articulated to the petiole, leaving a circular orifice for the passage of the œsophagus and the central nervous chain, as the prosternum does in front.

EPINOTUM. The fourth part of the thorax, the epinotum so named by the Emery, is dorsal only: it is supplementary and has no *sternum*, but it covers the metasternum. The epinotum appears to be more or less peculiar to the ants. Plate I *a* (*Myrmecia aberrans*) shows it as a red rectangle, long and narrow behind the mesonotum, which is dark-coloured, and the deep transverse line which represents the metanotum. In fig. 5 it extends as a long groove from the metanotal hollow which adjoins the mesonotum, as far as the articulation of the petiole, which adjoins the thorax. The epinotum varies enormously. It very often has teeth or spines behind, as in Plate II *c*. Sometimes it bears a single sword-point in the middle, as we see in Plate IV *f* (Part II) ; sometimes also a cone, as in fig. *e* of the same plate, and in *Iridomyrmex conifer* of Western Australia. A cone of this sort may even be bifurcated, as in *Dolichoderus cuspidatus*. The spines may be very long or curved in the form of a hook, as in Plate VIII, fig. *b* (Part III), and Plate XV, fig. *b* (Part V), etc.

Front and back, the epinotum has two surfaces, more or less distinct, which are usually separated from each other by spines, teeth or angles : 1 the surface known as *basal*, which is dorsal and immediately adjacent to the metanotum (or the mesonotum when the metanotum is absent); 2 the sloping surface, which ends with the articulation of the petiole. This last slopes backwards, being sometimes flat, sometimes convex, and sometimes also concave : on each side it has a respiratory stigma, as has the metanotum. Like the basal surface, the sloping surface is often provided with an angular edge, which separates it from the sides and from the metasternum (*episterna*). In Plate I, fig. *a*, the basal surface alone appears. In fig. 5, the basal surface passes without any distinct limit into the sloping surface, because the longitudinal section is made between the two spines of *Myrmica*. In Plate 1, fig. *c* (*Phyracaces singularis*), the large flat basal surface has a distinct convex lateral edge, and two teeth separate it from the sloping surface behind; on the other hand, no sharp suture separates it either from the mesonotum or from a metanotum which has entirely disappeared; the whole back of the thorax is welded together, but edged at the side. In Plate II, fig. *c*, this same epinotum is convex, narrow, and not edged at all along its basal surface as far as the long spines.

In the winged sexes, the boldly raised mesonotum shortens the basal surface of the epinotum and raises its sloping surface, especially in the ♀. Furthermore, when the teeth and spines of the epinotum are found in the worker, they are generally shorter and more massive in the ♀, and often entirely absent in the ♂.

WINGS. The winged sexes in the ants have two pairs of unequal wings, both articulated at the sides of the mesonotum, as we said before; they are depicted in figs. *k* and *m*, Plate III. The upper wings, which are also anterior, are stronger, longer and more important. The lower and posterior wings serve only to sustain the insect during flight. Hidden under the chitinous skin of the mesonotum, the strong muscles of the wings vary according to the weight of the creatures they have to raise, and the duration and

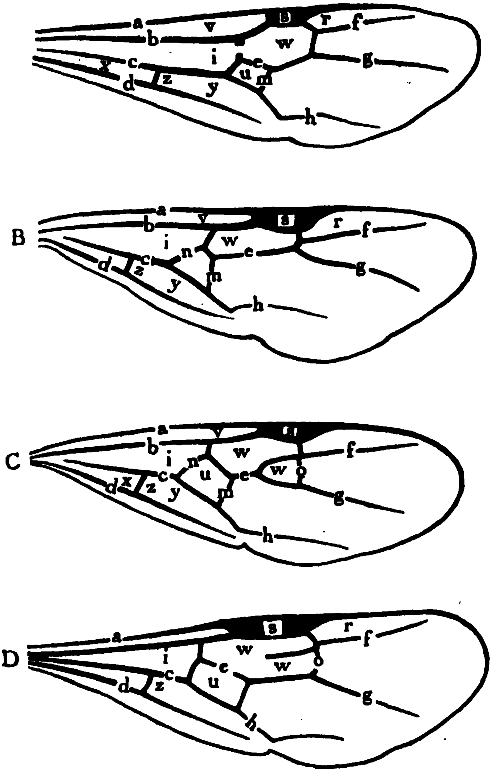


Fig. 7

height of the flight. They are especially powerful in the large and heavy ♀, which mate while on the wing, bearing their numerous spouses on their backs, as in the case of European *Lasius*.

Figs. 7, *A*, *B*, *C* and *D* represent the upper wing found in four different kinds of ants.

I do not wish to weary you, dear reader, with a detailed description of the various brown nerves in these wings, nor of the transparent cells, open or closed, which you see between them. If you are interested, you have only to study their names in the explanation of the figures. These names serve in particular to describe the various species. Here I will content myself with a few words. The small letters always signify the same nerve-threads and cells in the types *A*, *B*, *C* and *D* of each genus.

s denotes the black *marginal* spot, which is scarcely ever lacking in the fore-wing. Underneath is a closed cubital cell (*w*) which can be single (fig. *A* and *B*) double (fig. *C*) or divided (fig. *D* in *Myrmica*). Between the marginal spot and the extremity of the wing is a cell *r*, described as *radial*, which may be wide or slightly open, or even entirely closed. Under the cubital cell, a little way behind, appears another cell *u*, described as discoidal, etc. This will suffice to show my readers that the veins and cells of the fore-wings present distinctive characteristics which are of the utmost importance for the classification of ants into their various genera.

But in the hind-wing the venation is simpler and of no use in classification. Often the veins are atrophied. This is also the case with the fore-wing, especially in certain small species where it is not uncommon for the first or *marginal* vein to subsist alone with the marginal spot. But the most extreme case is that of the *Leptanilla minuscula*, ♂ which will appear in fig. 109 *B*, of Part V. In this creature, all the veins of the two pairs of wings have disappeared. Scarcely anything remains of them but small adjacent hairs.

In the ♂ ant the wings are articulated to the mesonotum just as solidly as in the other Hymenoptera (bees, wasps, etc.), while those of the ♀ are lightly attached and fall very easily. Indeed, whereas every ♂ ant dies shortly after copulation, the fertilized ♀ has many years of hermit-life to live within the nest. Hence as soon as she has been fertilized, she herself uses her legs to get rid of the wings which have become useless to her. Then as Janet has proved, the large muscles of her mesonotum are absorbed in her blood, where they are transformed into food for the mother and her brood, as we shall see later, in order that nothing may be lost.

LEGS. Ants have three pairs of legs, anterior, intermediate and posterior. Each of them is divided into five parts, articulated with each other in the following order, from the base to the extremity : 1 *the coxa*, 2 *the trochanter*, 3 *the thigh*, 4 *the tibia*, 5 *the tarsus*. All these can be seen in our plates and figures, and especially well in those which show the ant in profile (*e.g.*, Plate III *e*, and *g*, and *h*, Plate I).

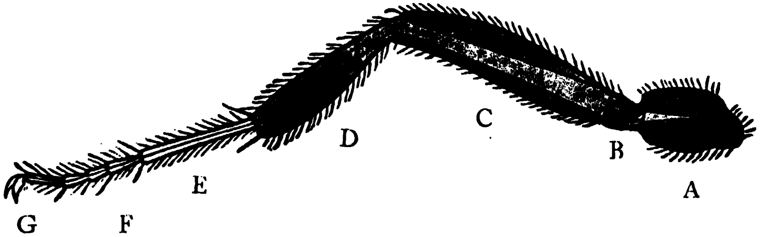


Fig. 8

COXA, fig. 8 *A*. The coxa is usually broad in the upper part, near the sternum, to which it is articulated, but is as a rule constricted at the base near its articulation with the trochanter. But it may be long, short, or flattened in one direction to correspond with a flattening of the thighs and tibiæ, or of the first alone. In this case especially it is then often hollowed out into a cavity of varying depth and width in order to receive the thighs when the latter are folded back. This is apparent in various ♂ of *Dorylus* and *Ænictus*, for example (see fig. 107 *A* in Part V). Obviously legs of this kind can only be moved in one direction when they are folded thus.

TROCHANTER, fig. 8 *B*. This is a little joint, more or less spherical or slightly elongated, which is intercalated between the coxa and the thigh and articulated with both. In my opinion its purpose is to enable the legs to move in all directions, as much by means of its articulation with the haunch as by that with the thigh. Indeed where the two last are flattened, the trochanter is not, or only so to a small extent. Thus when the legs fold back it may cause them to move in directions in which the other articulations (the coxa upon the sternum, the thigh upon the tibia, or tibia upon the tarsus) cannot move or can only move partially, since they are articulated somewhat like our elbows or knees, and not like our shoulders.

THIGH, fig. 8 *C*. The articulation of the thigh with the trochanter has just been described, and that with the tibia is a simple knee. The thighs may be folded back against the base of the coxa by means of the trochanter, and at the extremity against the tibia, but it is rather the latter which may be said to fold back upon them. The thighs are often flattened, as we shall see in fig. 107 *A* (Part V), but may also be enlarged, especially towards the extremity; as in Plate II, fig. *a*, and sometimes much more still. It is the thighs and the tibiæ which chiefly determine the length of the legs as a whole, and this varies extremely. It is only necessary to compare in this respect figs. *b* and *c* of Plate II; in this last, we find a pointed tooth on either side of the knee, terminating in the thigh at its junction with the tibia. Thighs and tibiæ shortened, thickened or flattened in a certain direction, like those of *Lasius* (*Acanthomyops*) *latipes* ♀, which appears in fig. 86 (Part III), may also serve for grubbing in the ground.

TIBIA, fig. 8 *D*. The tibia forms an elbow with the thigh, as we have just explained, and is sometimes flattened in a similar fashion, more rarely swollen, as we shall see in fig. 87 (Part III). It generally broadens out a little from the base to the extremity, and frequently has strong hairs or bristles, especially on the side which bends over the thigh; frequently there are one or two particularly strong ones near the extremity. But the most important appendage of the tibia is the *spur*, which is articulated at its lower extremity as shown in fig. 9 *B*. The spur has no muscles, and can only move when the first joint of the tarsus (*E*) bends with the tibia, at whose extremity lie the muscles which move the tarsus. On the other hand, the spur is adorned on the tarsus side with a charming *comb* (*F*) whose firm hairs grow shorter from the base to the tip. This comb comes in contact with the inner concave edge of the first joint of the tarsus, which is opposite to it and is also adorned with a sort of brush, with hairs similar to the sensory hairs (according to Janet). They are hollow, and lubricated by the tarsal glands. Thus the ants perform their own toilet, as Heinrich has so admirably illustrated in fig. 78, Part III. They draw their antennæ and their other legs between the comb on the spur of the tibia and the brush on the first joint of the tarsus of their anterior legs.

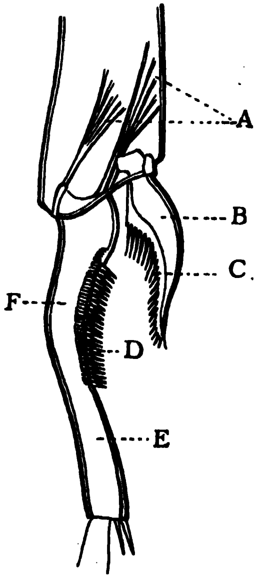


Fig. 9

At the same time the middle and hind-legs, though they have no concavity in the first joint of the tarsus, also possess

—as a general rule, at any rate—a more or less well-developed spur, sometimes even double, but frequently atrophied to such an extent that it no longer has a comb. The comb and brush are never absent from the fore-legs. The secretion of the glands of the tarsus causes the grains of dust and other impurities to adhere to each other, and this makes it easier for the ant to dispose of them with its comb and brush.

TARSUS (fig. 8 *E*, *F*, *G*). In speaking of the spur of the anterior tibia, we have already had occasion to mention the first joint of the tarsus, which is generally long, but there are four shorter ones following this. In *Melissotarsus* (fig. 87, in Part III), the first joint shows a remarkable modification: it is short and extraordinarily thick, but this does not prevent it from having a brush for cleaning purposes, with the aid of a comb on the spur of the tibia. In certain species which live on trees and plant ant-gardens upon them with the aid of plant-parasites, especially those of the sub-genus *Camponotus* which I have called *Myrmotarsus*, as well as in certain species of the sub-genus *Myrmothrix*, the tarsi, especially those of the fore-legs, are dilated and covered underneath with a thick brush of short, coarse hairs. Hairs of this kind, but less dense and noticeable, are often seen on the underside of the tarsi. I presume that they help the ants to keep a firm hold upon their airy nests.

The three intermediate joints of the tarsus are short, and have no outstanding features apart from fairly frequent brushes and spines. The last joint, on the other hand, which is a little longer, terminates in a double hooked claw (*G*, fig. 8), sometimes bifid (two-pointed), which enables the ant to cling to grass, vertical walls, etc. These tarsal claws are particularly well-developed in Emery's Australian genus *Onychomyrmex*. Between them lies a small pad called

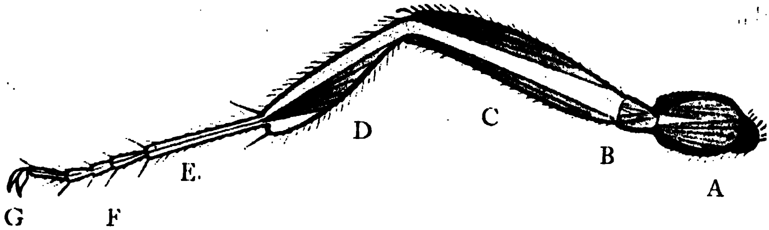


Fig. 8 repeated

the *empodium*. The tarsi are rarely flattened, but nevertheless their first joint is often fairly compressed.

3 PEDICEL

The narrow pedicel which separates the thorax from the abdomen and which distinguishes all the ants from allied Hymenoptera, belongs by phylogeny to the abdomen itself. It consists of one or two abdominal articles, separated from the others by an extreme constriction. Consequently the abdomen proper, which in other Hymenoptera is composed of six segments in the ♀ and seven in the ♂, does not possess more than five (or six) in the ants whose pedicel consists of a single joint or more than four (perhaps five) in those whose pedicel consists of two. The ♂ always has one more segment or joint in his abdomen than the ☿, the ♃ and the ♀.

That being understood, we may add that the first (anterior) joint or knot of the pedicel is called the *petiole*, and the second, which is posterior to the first when it exists the *postpetiole*. Now the petiole, which is constricted in front, exists in all ants, whereas the postpetiole shows all possible transitions between total or partial constriction and total fusion with the abdomen proper. Furthermore, in the genus *Eciton*, the worker (fig. 108, Part V) has a petiole and postpetiole which are equally narrow and equally distinct, whereas the ♂ of the same species possess a petiole only, the abdomen absorbing the petiole, just as it does in the case of the ♂ of its relation *Dorylus* (fig. 107 *A*, Part 5). The postpetiole may therefore have a share in sexual polymorphism—which complicates things considerably.

My readers will judge of the matter by comparing the following figures in Part I:—

1 A single petiole surmounted by a scale: Plate III, fig. *k*, *l*, *m* and *n*.

2 A petiole and postpetiole which are equally constricted: Plate II, fig. *a*, *b* and *c*; Plate III, fig. *a*, *b*, *c*, *h* and *i*: then fig. 5, which shows a longitudinal section of *Myrmica*. *K* shows a constricted postpetiole, absolutely distinct; the petiole is the constricted nodiform segment which precedes it.

3 A postpetiole which grows broader and broader behind in the order of the figures indicated: Plate I, figs. *a*, *b*, *c*; Plate III, figs. *f*, *g*, *d*, *e*.

This last figure represents the wingless ♀ of *Leptogenys* (*Lopobelta*) *Iheringi*; here the postpetiole has almost become once more a mere abdominal segment; but in certain species of the sub-genus *Brachyponera*, the structure between the postpetiole and the abdomen proper shrinks to practically nothing—or even vanishes altogether. As in the other figures under the heading of No. 3 above, the petiole is not surmounted with a scale, raised and flattened in front and behind, but with a fairly thick node. These ants all belong to the sub-family of *Ponerinæ*, while those under the first heading belong to the *Formicinæ*. Nevertheless, even here we can see all the transitions; certain *Formicinæ* have a petiole in the form of a thick node and certain *Ponerinæ* have a scale.

The petiole and the postpetiole may both bear spines or teeth, lamellæ, and even certain appendages shaped like wings, exactly as the thorax does. These appendages may be paired or unpaired, and in the latter case they are situated in the middle. In the genus *Strumigenys*, the pedicel as well as the sloping surface of the epinotum possesses hard masses filled with air, like little soap bubbles imprisoned in the chitin; they have a peculiar appearance. Underneath the petiole and the postpetiole we often find teeth, lobes or spines turned obliquely in front and evidently destined to check any excessive forward motion of the abdomen.

On the other hand, the petiole and postpetiole of *Cremastogaster* (see Plate XIV *d*, Part V, and fig. 100, Part IV), as well as the scale of the petiole of many *Dolichoderinæ* (fig. 97, Part IV), are flattened underneath to give more freedom of movement. They protect themselves from their enemies by means of the poison in their abdomen which they curve back until it comes above their heads (*Cremastogaster*), or else they work it in all directions in order to sprinkle the enemy with liquid from their anal glands (*Tapinoma*, *Azteca*, *etc.*) as may be seen in the figures indicated.

In short, then, we see that the petiole and postpetiole of ants serve to augment the diversity and agility of their movements, at the same time preventing them in certain cases from becoming excessive. The petiole, postpetiole and abdomen also possess stridulatory organs (fig. 5 *K*) which consist of a series of transverse striæ producing a faint sound by means of the friction of the segments against one another. In our figure these ridges are shown in cross-section. In *Megaloponera* the stridulation is fairly powerful.

In order to simplify matters I would refer the reader to the following plates and figures, in addition to those already indicated. They show the peculiarities of the petiole and the postpetiole in various species:—

Plate IV, figs. *a*, *c*, *e*, *f*, *g*, *h* (Part II).

Plates VIII and IX (Part III).

Plates X, XI and XII (Part IV) show the movements of the ants in their warfare, and the role of the petiole, while Plate XIII pictures various forms of the scale. Fig. 99 represents a *Cremastogaster* with its abdomen first raised and then lowered side by side with an ant which has a scale (*Monacis*).

Plate XIV (Part V), figs. *a*, *b*, *c*, *e*, *f*, *h*, *k*, and all the figures of Plates XV and XVI.

In the *Proponerinæ*, which in my opinion contains the earliest ants of the sub-family *Ponerinæ*, the petiole is present but for the most part it is fastened to the abdomen behind instead of being separated from it—that is to say from the postpetiole—only by a narrow articulation. In this respect it resembles the *Mutillidæ*, the family next of kin to the ants. Plate III, Part V, shows one of these curious ants, *Mystrium Völtzkowi*.

4 Abdomen

The ant's abdomen has therefore four or five joints in the ♀, ♃ and ☿, and five or six in the ♂, according to whether the postpetiole is annexed to it or not. And the crop or social stomach, which cannot exist in a constricted postpetiole, may occur in the basal joint which corresponds to it in ants whose abdomen proper has five joints in the ☿, ♃ and ♀. and six in the ♂. Hence the structure of the abdomen partly depends on the constriction of the postpetiole. A glance at fig. 5, *K* and *L* (☿ with an abdomen consisting of four joints) and a comparison between this and figs. 14 *A* and 15 *A* (☿ with abdomen consisting of five joints) will be convincing in this respect.

Where there is no further constriction after the postpetiole, it becomes rounded in front in such a fashion that it appears as the first abdominal segment, and the following segment (fig. 5 *N*) as the second. The form of the abdomen varies less than that of the head and thorax. It can have a margin and even be lamellated in front, round or elliptical, sometimes even triangular and narrowed behind in such a way that it can be curved back (*Cremastogaster*).

The abdominal segments are fitted into one another in the following manner, so as to allow the abdomen to dilate as a whole.

Each segment is formed from a fairly hard but thin dorsal plate, made of elastic chitin, covering the ventral plate which is partially hidden beneath it. The two plates are joined to one another, behind and laterally, by a fine, supple membrane, broad and folded, or a transparent cuticle, visible from the outside only when the abdomen is greatly distended, as we shall see in an extreme form in figs. 80, 81 and 82 (Part III). The stridulatory apparatus is generally situated at the base of the segments, and this base is therefore mobile.

The last segment ends in a more or less obtuse point, which affords a passage to the *cloaca*. The latter is either circular or a transverse slit, according to the ends it has to serve.

In the ♀, the ♃ and the ☿, it is round and ciliated all over, as may be seen in fig. 27 in connection with the *Formicinæ*, which ejaculate their poison in a manner shown in Plate XII (Part IV). On the other hand, it consists of a transverse slit in the other sub-families which have a sting, or which ejaculate the secretion of their anal glands, as we see in fig. 5 of the present volume, or fig. 97 (Part IV). The cloaca therefore comprises or covers various openings : 1 the anus, from which excrement is ejected; 2 the vaginal opening, whence the eggs come through the oviducts, before hatching, and the spermatozoids through the seminal vesicles of the ♀, as we shall see later; 3 the sting, or opening of the poison glands as they appear in fig. 21 *B*, *C*, *E*, *F* and *G*, fig. 22, *F* and *I*, and fig. 20 *C* and *D*. The internal structure of the organs which empty themselves into the cloaca will be dealt with in connection with the internal anatomy. The sting may be very long and powerful (fig. 5 *R* and 20 *F*) or may have been gradually weakened, almost to the point of complete atrophy, as in *Bothriomyrmex* and most of the *Dolichoderinæ*, or it may be *transformed* into a supporting apparatus for the orifice of the vesicle, as in fig. 21, *E*, *B*, *F*, *G*, in the *Formicinæ*.

The second and third of these openings are present in the ☿, ♀ and ♃, but lacking in the ♂, which never has a sting or poison. On the other hand, a large opening beside the anus contains the external male organs of fertilization. Fig. 10, *F*, *G*, *H* and *I* show those which belong to the external anatomy, and which consist of solid chitin, reddish, brown or black. At the moment of copulation, all these organs are simultaneously thrust out by a forward movement of the last abdominal segment enclosing them; they open and afford passage to the *sagittæ* or genital valves, which constitute a penis or double rod, and which enters the vagina to deposit its semen. The sagittæ are covered (*I*, fig. 10) by a second pair of intermediate genital valves called *volsellæ* (fig. 23 *H*): and the volsellæ are in their turn covered by a third external pair called *stipites* (23 *G*). At the base of these last, and fused with each of them, is a broad piece, the scale, which is not indicated in the diagram. Underneath all the rest, and situated in the middle, is a transverse sternal plate, the annular lamina, which is hollowed out in the middle and can be prolonged, in the *Dorylinæ* especially, into a long *subgenital* lamina. *E* in fig. 10 shows the ejaculatory duct. Lastly, in many ♂ ants, we find under the *pygidium* or dorsal plate of the last abdominal segment, small single-jointed hairy appendages called the *cerci*, which are directed backwards. The central plate of the last abdominal segment is often called the *hypopygium*.

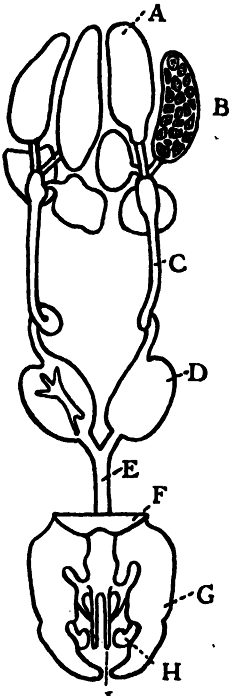


Fig. 10

5 SCULPTURE, HAIRS, PUBESCENCE AND COLOUR

We have at last finished with the details of the ant's extremely variable body, but in addition to the interior with which we shall deal afterwards, we have still to describe the surface, which presents numerous strange peculiarities, often very striking to the eye. Follow me, therefore, with patience into this world of variations. The structure of the body may be sculptured or chiselled in various ways: it may be provided with hairs, scales or clubs (pilosity), erect or appressed (pubescence) and lastly it may be of all the colours and shades imaginable. We will proceed in correct order.

SCULPTURE. When the chitin is really smooth it is also *shiny*. Whenever we find that it is unpolished or merely silky we may be sure that there is some sculpture, more or less microscopic but distinguishable under a strong magnifying glass. Sculpture of this sort may cause the body to appear grained, silky, stippled, striate, rugose, etc., according to its nature and minuteness. Rough sculpture, like that in Plate I, fig. *a*, is visible to the naked eye.

STRIÆ (Plate I, fig. *a*, *Myrmecia aberrans*). The striæ are regular, the deep lines alternating with elevations or ribs as regular as themselves, but sometimes it is the raised rib and sometimes the deep line which shows more clearly. Our *Myrmecia* in fig. *a* is striate lengthwise on the head and crosswise on the epinotum and petiole, while it is smooth on the postpetiole and abdomen. On the pronotum we notice large striæ diverging behind. But on looking carefully at the striæ on the pronotum, we see that they are not only finer but also slightly sinuous and less regular, tending to become wrinkles.

WRINKLES. Plate I, fig. *b* shows the petiole of *Pristomyrmex mandibularis*, which is coarsely wrinkled lengthwise. Not only are the wrinkles generally sinuous, but they have more or less distinct passages, raised and transverse, running between them. Thus there are transitions from the striped to the wrinkled type on the one hand, and from the wrinkled to the following type on the other.

RUGOSITY. When the transverse connecting links of the wrinkles increase more and more in number and size, and furthermore become uneven, we have what is known as rugose sculpture, composed of raised and sunken portions which are at the same time longitudinal and transverse, and which cross each other more or less irregularly. The sunken portions then become pits, either long or round in shape, and divided in all directions by the wrinkles thus split up. This is the case with the basal surface of the epinotum in Plate 1 fig. *b* (*Pristomyrmecia*).

RETICULATIONS. When the rugosity becomes regular, meshes are formed, meshes, more or less rectangular in shape, whose sunken portions are flattened to some extent at their base. They are then called reticulations. The finely reticulated ant is generally silky or, as we say, *subopaque.*

PITS AND PUNCTATION. When the coarse rugosities become regular, and at the same time remain deep, concave and very dense, and when their intervals are slightly flattened instead of remaining raised, we use the term pits. When this form of sculpture is at the same time dense and fine, we call it punctation. Dense punctation renders the insect matt. Sometimes it is microscopic.

But where the pits or sunken points are more and more widely spaced, the chitin separating them ceases to be raised and even grows smooth again in proportion to the increase in the size of the spaces. We then speak of the pits or points as discrete or scattered. A silky or subopaque aspect may result from fine reticulations or very fine points which are beginning to appear spaced, according to circumstances.

TRANSITIONS. Between these various kinds of sculpture we find all possible combinations and transitions. Thus there may be a very fine, dense punctation between coarse wrinkles or coarse spaced pits, etc.

But there are also transitions between the sculpture and the form of the body. In the *Attini*, the ants which grow mushrooms, we often see little indentations and tubercles and other asperities on the body and limbs, in such large numbers that they form a transition-stage to sculpture, becoming more and more closely compressed, regular and minute. A similar phenomenon is found on the legs of the *Cryptocerini.*

We shall see yet other curious transitions between sculpture, hair and pubescence—so true is it, dear reader, that we know of nothing absolute on this earth. Everything is relative and transitory, in slow evolution. Hairs may be transformed into quills, and these again into spines or teeth. They may thicken and become clubs, fall recumbent and become pubescence or scales, or grow hollow inside and come in contact with the organs of sense or the glands; finally they may return to the interior and be transformed into curious organs of which we shall speak later.

ERECT HAIRS. The erect hairs of *pilosity* may be absent, bristling, thinly scattered, dense, oblique, very fine, coarse, short, long or transformed as we have just said. They can also vary in quantity, colour and quality in different parts of the body and the extremities (legs, antennæ, etc.).

Hairs are generally pointed at their extremities, but they can also be fairly blunt and even jagged. Fine pilosity sometimes has a woolly appearance, often owing to the fact that a hair is divided at its base into three or five other very fine hairs, as in the genus *Triglyphothrix*, which I have so christened for that very reason. In *Echinopla melanarctos*, the whole body has an uneven sculpture bristling with little cylinders, each about one-tenth of a millimetre high and one-thirtieth of a millimetre thick. Each of these columns is equally thick at its base and its extremity, which is truncated and bears a long black hair, thick at the bottom but pointed towards the tip. This ant has the appearance of a diminutive hedgehog.

Many *Strumigenys* bear in the guise of hairs little oblong clubs which are usually short and standing up on end, but sometimes perched at the extremity of a long hair. I leave my readers to study the pilosities of ants for themselves in the figures which represent them.

PUBESCENCE. As it becomes more and more oblique, the pilosity of the ants gradually turns into pubescence, where the hairs are entirely contiguous. This can also be more or less rare or dense. In the first case it forms a fleece which then gives its colour to the ant. But the pubescence may also consist of thick, fine hairs, as well as flattened hairs transformed into oval scales. Scales of this sort may be found at the bottom of a pit, as in certain *Cryptocerus*, and be hollowed and surmounted by a ridge placed lengthwise. Like fine sculpture, pubescence tends to render an ant more or less silky, ashen or matt.

Plate X *b* (Part IV), and Plates XV *b* and *c* (Part V), give the reader an idea of the fleeces which cover the bodies of ants, in their various beautiful colours. That of Plate IX *c*, Part III, is composed of a very coarse pubescence which is absent in the middle segments of the abdomen.

With regard to the antennæ (see 'Head'), we have mentioned the clubs which contain the organs of topochemical smell.

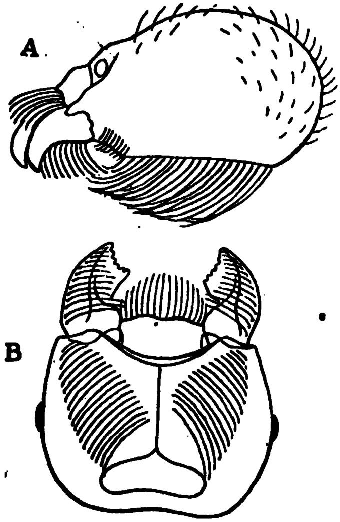


Fig. 11

These are erect or contiguous hairs, more or less thick or flattened, but containing sensory nerve-cells. They can be seen in fig. 23, *A*, *B*, *C* and *D*, and we shall return to them later.

PSAMMOPHORES. Following Santschi, we give this name to the rows of long hairs, equal in length, one of which is situated under the sides of the head, another under the mandibles, another at the edge of the clypeus, where it is used to pick up the grains of sand which the ants living in deserts throw out of their nests. They are shown in fig. 11, *A* and *B*.

COLOUR. All the external organs of the ants, as well as the erect and prostrate hairs, have their special colour. As with other animals, these colours are on the whole brighter in the tropics than in cold countries. As a general rule, they grow paler in forms which live underground. Australia, in particular, is the home of ants with brilliant metallic colours, as we see in Plate IX *a* (Part III). We have already spoken of the magnificent fleeces often presented by pubescence, from which the ant then takes its colour. Often also there is a metallic lustre on each of the scales mentioned above, as well as upon the iridescent wings or certain pubescences of gold, silver, and reddish-brown. When exquisite sculpture is united with harmonious effects of metallic colour and pubescence—as in *Chariomyrma Hookeri*, Plate XIII *b* (Part IV)—the ants may arouse admiration as veritable gems.

The rarest colours in ants are green and pure white, but even these are sometimes seen. The most common, on the other hand, are reddish-brown, black, brown and yellow. Metallic blue is rare, and the pure red seen in Plate I *a* is not common. A grey effect is most frequently produced by pubescence. In Africa, especially the tropical parts, black is predominant. In Europe, colours as well as forms are monotonous; near our own homes, we see scarcely any ants except the black, brown, reddish-brown and yellow—sometimes with grey fleece. At the same time, I must repeat that in many cases the shades of the various parts of the body offer variety and contrast, even among themselves.

Chapter IV

INTERNAL ANATOMY

We will divide the internal anatomy of ants into ten parts:—1 Cuticula, 2 Intestinal canal, 3 Internal genital apparatus, 4 Respiration, 5 Circulation, peritoneum and fat-body, 6 Poison apparatus, 7 Other glands, 8 Nervous system, 9 Special senses, 10 Muscles.

1 Cuticula

As we said before, hard chitin is at the same time the ant's skin and skeleton, to which the muscles are attached. Like ourselves, ants have an *epidermis* or outer chitinous skin, which we have just been studying, and internal skins, corresponding to the *epithelium* of our internal mucous membranes, like those of our mouth, intestines, bronchial tubes, etc. The internal skins of the ants are known as *cuticulæ*. They are generally extremely fine and transparent, secreted by flat cells each containing a nucleus.

Let the reader glance at fig. 12. It represents a microscopic cross-section of the gizzard (curved back) of a very small ant, and the crop which covers it; the interior of the gizzard being seen in the centre. *A* shows the cuticula of the gizzard, which has become hard, thick and chitinous; it is covered by numerous little nuclei in the form of black spindles, between which lies a very fine, greyish substance, the protoplasm of the cells. At *I* is seen an irregular line which indicates this cuticula when it has become thin and transparent, and has turned in the opposite direction. Under this, *H* shows the little nuclei of the generative cells, which are much more widely spaced than those of *A*, for they have much less to secrete. *K* indicates the very thin cuticula of the crop, which is turned back again in the same direction as *A*, but here the nuclei are so widely spaced that only four of them can be seen on a whole side, and their cellular substance is so tenuous that lithography is unable to reproduce it. *M*, on the other hand, shows under the thick, chitinous sepals of the gizzard numerous round nuclei and the fairly thick protoplasm of their cells which secrete the sepal.

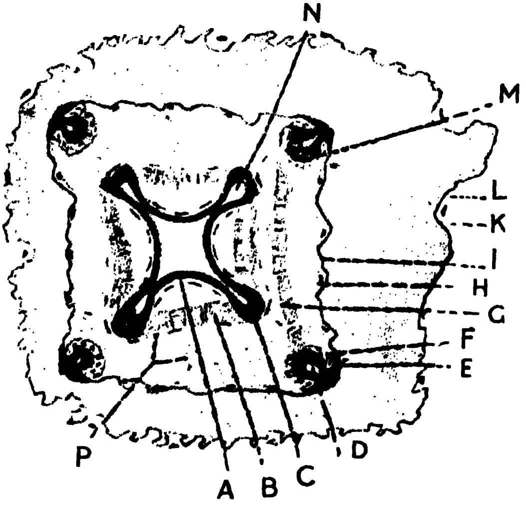


Fig. 12

As my reader will be aware, the body of every living being is composed of microscopic cells whose nucleus is surrounded by a certain amount of nutritive protoplasm ; we mentioned this when discussing the egg in Chapter II. These cells serve as a microscopic factory for a host of chemical products, varying according to the organ, and their composition varies in consequence, as we shall see in connection with the glands. The cells which produce the cuticulæ have generally one function only—to secrete chitin, which is therefore only a thickened cuticula, as figure 12 clearly shows. And the hard carapaces of beetles simply have beneath them cells of corresponding thickness, by which they are secreted.

At the opposite extreme we may consider fig. 13, which shows in *A*, *B*, *C* and *D* a very highly magnified representation of the excretory duct of a gland. *D* represents the cuticula, *A* the cells by which it is secreted, *B* the nucleus of the cells and *C* the contents of the duct, that is, the secretion. But the duct has little branches, each of which leads to a single cell, whose functions we shall discover later. All the cuticula of branch *E* of the duct is secreted by a single cell, whose protoplasm (*G*) surrounds the whole branch entirely by itself. Its nucleus, elongated like a spindle, is denoted by *F*. In this way I hope to explain to my readers the all-important rôle of the *matrix* cells of an insect's cuticula. This role has been admirably described by Leydig. The cuticulæ cover, to a certain extent, nearly

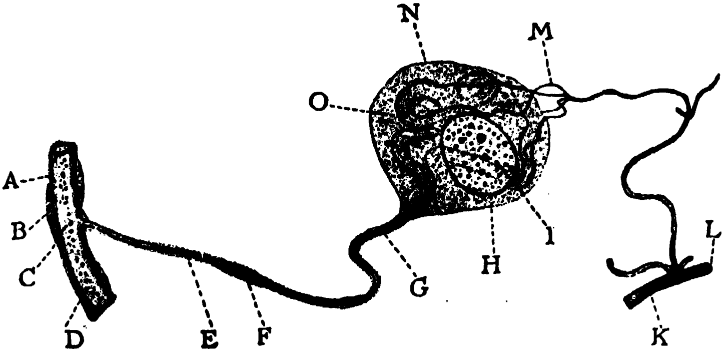


Fig. 13

all the external and internal parts of the bodies of insects which are not bathed in their blood. Hence it was essential to begin with them.

2 INTESTINAL CANAL

During our discussion of the head, jaws and tongue, we mentioned the mouth, buccal sac and lips. The section represented in fig. 5 (p. 49) shows the *pharynx*, or entrance to the intestinal canal, between *A* and *d*. By way of this canal every ant swallows whatever it sucks or licks up with its tongue, after tasting it. We must not forget the great mobility of the tongue (*b*) which can be voluntarily protruded or withdrawn, along with the chin (*Z*) and the jaws.

Thus the *œsophagus* leads from its opening to the *pharynx* B, fig. 5, into which is poured the secretion of the maxilliary glands (*C*) the mandibular glands (*D*), then the pharyngeal gland (*E*). The œsophagus proper afterwards continues in the form of a narrow tube (*H*), covered with its cuticula all the way along the thorax and the pedicel, as far as the abdomen proper. After the pharynx, the œsophagus crosses the brain, which has a major or super-œsophageal ganglion and a minor or sub-œsophageal ganglion. In short, the sole purpose of the œsophagus is to transmit directly and immediately to the crop the food which the ant has swallowed with the aid of the muscles of the pharynx.

The *crop*, denoted by *L* in fig. 5 and by *A* in figs. 14 and 15, is the social food-reservoir of the ants. It is an organ of first-rate importance. Figs. 80, 81 and 82 (Part III) show the amazing distension which an ant's crop may exert upon the plates of the abdomen which contain it, entirely for the purpose of feeding the colony, that is, the society. In certain species we often find floating about the crop a hard mass of food, which has evidently become coagulated and unable to find a way out on either side.

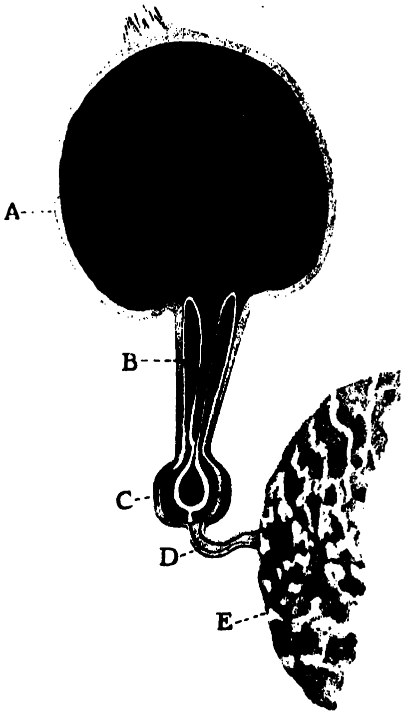


Fig. 14

The crop is completely surrounded by weak muscle fibres: but it is not these which compress it when the ant disgorges honey-dew to its companions, but rather the whole system of muscles partially represented in fig. 27, which squeeze the entire abdomen while the ant opens its mouth. The walls of the crop have no digestive gland in addition to the cuticula. This organ is merely a recipient, as clean as possible, which does not in any way alter the food it contains, and passes it on in its original form by regurgitation. It is the crop which normally distends the abdomen of the ☿, whereas that of the ♀ is often distended by ovaries full of eggs.

Fig. 14 *A* shows a crop full of honey coloured black, while the closed gizzard *C* prevents the smallest particle from passing into the ant's digestive stomach, denoted by *E*.

The *gizzard* or *pumping stomach* of the ant is shown in *B*, fig. 15, in *B*, *C* and *D* in fig. 14 and in transverse section in figs. 12 and 16. This is certainly the most curious and characteristic of the ant's internal organs. It serves to close and open this intestinal passage at will, for the purpose of separating the social and individual food-supply from each other. It may be divided into two parts: 1 the *anterior portion* pictured in *B*, *C* and *D*, fig. 14; 2 the *posterior portion* or knob, enclosed in the stomach, which is pictured in fig. 17, and is identical in all ants.

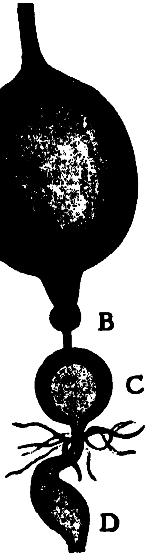


Fig. 15

The anterior part varies enormously with the sub-families and their groups. Uniform in the *Ponerinæ*, *Dorylinæ* and most of the *Myrmicinæ*, it is all the more curious in the *Formicinæ*, *Dolichoderinæ* and certain *Myrmicinæ*. In the present brief description, I am concerned with its phylogeny, and hence I will begin with species in which it is uniform—the *Ponerinæ*, for example. Strange to say, the structure of the gizzard is everywhere the same in the ☿, the ♀, the ♂ and the ♃ of each species.

In the *Ponerinæ*, etc. the anterior part of the gizzard consists of a simple tube, exactly like *D* (fig. 14). But this tube is larger, surrounded by strong circular muscles, and contains in its interior four large longitudinal folds of slightly thickened cuticula. When the circular muscles contract, the four folds are brought together and close the entrance to the gizzard. Viewed from the anterior end, a gizzard of this type shows an internal gap, more or less distinctly cruciform, between its four longitudinal folds, and bordered by the cuticle. Emery considers that this primitive form of gizzard exemplifies the simple movements which are called peristaltic, similar to those of our intestines, which alternately open and close the parts of the tube and are thus able to pump up small portions of alimentary substance and gradually pass it on from the social crop to the egoistic and individual stomach.

Passing on to more complex forms, we find even in the genus *Dolichoderus* that the tube divides into a posterior part with a larger oval space and an anterior part with a narrower tube, the whole forming a canal.

Now let us consider the *Formicinæ* (fig. 14). Here I have myself divided into four parts that portion of the gizzard which is visible from the outside: a *middle portion* (*D*), *bulb* (*C*) corresponding to the posterior space in *Dolichoderus*, *valves* (narrow part between *C* and *B*) and *sepals* (*B*), corresponding to the valves in the narrow anterior part of the *Dolichoderus*. The sepals are four in number, corresponding to the four folds in the *Ponerinæ*, etc.; only two of them appear in the picture. They are chitinous, but linked together by a thin cuticle, continuous with that of the crop. Between them lies a wide space, which I have called the *calyx*. I would ask the reader to look at fig. 12, where *F* represents the body of a sepal (curved and turned back it is true, but here this makes no difference) in cross section, *E* the lateral wings terminating at the cuticle, and *D* the longitudinal groove which contains the body of the sepal. What does all this signify?

My readers will notice everywhere a fourfold symmetry. In fig. 15 *B*, one of the open sepals is shown in front, in the middle, and another at each side; the fourth is behind. In fig. 14 (see the crop) it is obvious that the calyx is still full of dark honey as far as its narrow base. Imagine this base cut through obliquely, and you have fig. 16. The line $\phi\omega$ in this figure represents the exact centre of the gizzard of *Camponotus ligniperdus*, situated behind the two sepals seen in fig. 14, and continued on the two corresponding sides of the valvular constriction and the bulb. Here is an explanation of it :

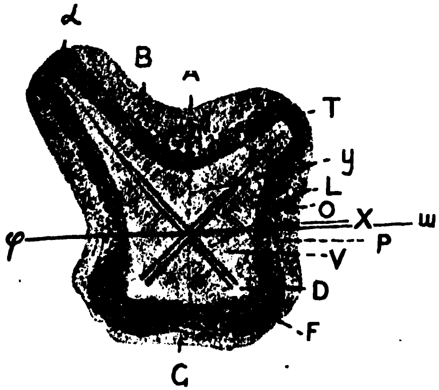


Fig. 16

Fig. 16 being a cross-section, the base of two sepals is shown on one side *φω*; their body is denoted by *F*, and the section of their longitudinal groove by *D* ; on the other side is the beginning of the bulb, while *α* stands for the chitin (cuticula) of one of the sides of the bulb, and *A* for that of its concave part. In the middle, between *ω* and *φ*, a distinct cross *X* represents the insterstice between the four valves almost closed. Lower down, in the bulb, this interstice opens, as is seen in another sort of gizzard shown in fig. 12. *L*, *G* and *B* show the strong transverse muscles which cover the sepals and especially the bulb of the gizzard. The cells of the matrix or epithelium which secretes the cuticula, that is, the chitin of the gizzard, are denoted by *O*. The weak longitudinal muscles of the gizzard, to which I once attributed the power of opening the valves, is indicated by *P*, on the concave side of the bulb (between *O* and *L*). The tendons (*T*) of the transverse muscles are represented on each side and on each sepal. Lastly, *V* shows the four triangular valves which close the gizzard between the sepals and the bulb.

The four valves are therefore the most important part, and this alone, as we see, is capable of being hermetically sealed. In *Camponotus*, the calyx with its sepals acts as a posterior funnel to the crop. The bulb (*C* fig. 14) with its four raised sides and four concavities possesses, as we have just said, an interior space (fig. 12) which remains open behind, near the tube of the middle portion (*D* fig. 14). This last has a cuticula, like the knob of the posterior part of the gizzard, which is hidden in the stomach (fig. 17 *E* and *I*).

When the internal lining which extends from the mouth to the gizzard, and whose ordinary calibre and cylindrical form are preserved almost completely in the knob, reaches the extremity of the projection, it turns upward abruptly, and is reflected back to form the external envelope (cuticula) of the knob (fig. 17 *E*), which thus has a homogeneous shiny appearance. When it reaches the large gastric cells (fig. 17 *D*), this cuticula grows thinner and disappears. *The stomach has no internal chitinous lining.* Needless to say, the place where the internal lining of the knob turns upward forms the orifice of the gizzard in the stomach. Between the two cuticulæ of the knob we naturally find their matrix, turned upward in a similar manner, which is directly contiguous to the large gland-cells of the stomach. To make a convincing examination of these facts, the muscles, cells, etc. must be destroyed by means of a drop of caustic potash solution. The chitinous lining, which, as is well known, is quite resistant to this reagent, then shows up very clearly. Using a preparation of this kind, and drawing gently under the microscope the anterior part of the gizzard, while the stomach was fixed, I have successfully turned back the whole cuticula of the knob under my eyes, thus making the knob disappear or rather change into a simple chitinous, cuticular tube entirely outside the stomach. This tube could then no longer be distinguished from the cuticula of the central cylindrical part of the gizzard, which merely appeared to have doubled in length. The knob varies in length according to the species.

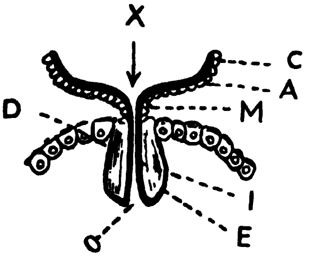


Fig. 17

Fig. 17 represents the knob of the gizzard of *Dorymyrmex* (*Conomyrma*) *pyramicus* in longitudinal section, opening at *O* into the stomach, which hides it. *X* shows the point at which it comes out of the bulb of the gizzard, *I* shows its internal cuticula turned upward again, dwindling away and coming to an end between the large digestive cells of the stomach (*D*). *M* indicates the middle part of the gizzard, which in this genus is very short. Lastly, *C* represents one side of the bulb and *A* the matrix of its cuticula or its tendons.

This brings us to other forms of gizzards. In the genus *Prenolepis* and related genera, the four sepals curve back towards their extremity, turning back and bearing with them the walls of the crop. The transverse muscles, however, do not fold back, but cover all the folded part of the sepals, so that the gizzard remains separated from the crop by their means. The same obtains with nearly all the *Plagiolepidini* tribe, though in their case the sepals do not curve back but bend at an acute angle near their base, and thus themselves constitute the valves of the gizzard and the cruciform structure in which they close.

It is somewhat different with most of the *Dolichoderinæ*. When the sepals are present, they fold right back from their base and form valves; but the folded part has no strong, circular muscles covering it, and draws the walls of the crop with it. The crop then covers the anterior part of the gizzard, or even the whole of it if the sepals are long, as in *Iridomyrmex*. Then a single cross-section gives us the crop covering the folded sepals, which in their turn cover the bulb as we have described it above in connection with fig. 12, to which reference may be made. Remember, dear reader, that the whole *Bothriomyrmex* of fig. 12 is not 2 millimetres long, and that its gizzard occupies less than a tenth of a millimetre. Nevertheless, I have succeeded in my time in making five sections through it by the aid of a microtome. They are coloured with iodine and I still possess them.

Certain *Dolichoderinæ* have ceased to possess sepals, and others (*Dolichoderus*) have gizzards resembling those of the *Ponerinæ*. The primitive forms *Formicinæ* also have shortened and simplified gizzards, but even these have strong valves.

Lastly, *Cryptocerus* (*Myrmicinæ*) have in their crop an object like a perfectly rounded mushroom-head, which represents, more or less, the four valves of the gizzard, but which is irregular, chitinized, ramified in its intervalvular spaces and filled with microscopic stars (solidified folds). This gizzard is very different from all the others.

What, then, is the use of the bulb of the gizzard ? Emery has tried to explain this as follows, and I think that he is right :

He compares the bulb of the gizzard to a suction and forcing pump of india-rubber formed by the contraction of the transverse muscles in such a way that the four concave portions (fig. 12 *A*) situated between the four sides become much more concave still. Thus they almost meet in the middle and discharge into the individual stomach, through the tube of the middle portion, the greater part of the contents of the bulb. Meanwhile the valves, hermetically closed by their muscles, prevent any discharge into the crop in the opposite direction.

When, on the other hand, the ant wishes to eat on its own account, it relaxes the transverse muscles of the gizzard, which permits a small amount of nutritive honeydew to pass gradually from the calyx into the bulb between the valves.

Janet and Emery think that the muscles of the pharynx mentioned above have an action analogous to that of the gizzard. When an ant wishes to disgorge, it contracts the transverse muscles of the gizzard valves in order to prevent anything from entering the bulb, and on the other hand relaxes the muscles of the pharynx as it opens its mouth. This is the reverse of what it does after swallowing through this same mouth the food which it has licked and sucked up with its tongue. If this is the true state of affairs, as I believe it to be, it helps us to a better understanding of the rôle of the buccal sac (fig. 5 *d*) which we mentioned in connection with the external anatomy. It is used, generally at least, as a reservoir for the solid excrement which would otherwise be likely to encumber the crop and the valves of the gizzard.

Fig. 81 (Part III), will show how the crop of a ☿ nurse pitilessly relegates all the rest of the intestinal canal to the back, at the same time pressing it against the internal wall of the two last abdominal plates.

The *individual stomach* follows immediately after the posterior part of the gizzard, whose cuticle comes to an end as we have seen, and with which it is united. Its walls are provided on the inner side with large cells (fig. 17 *D*), which digest the food, for as soon as it enters—never before—it is decomposed. The stomach varies very little and has no other special interest. It may be seen in figs. 14 *E* and 15 *C*.

Immediately after the stomach come the urinary vessels or Malpighian tubes, which form a circle of slender filaments varying in number between 4 and 20, or even more. They are like those of other insects. The Malpighian tubes are arranged round the *small intestine*, which has another cuticle, like the œsophagus, etc. It is relatively very short, and is surrounded by circular muscles. The Malpighian vessels and the small intestine may be seen in fig. 5 *M* and fig. 15, between *C* and *D*.

The small intestine suddenly broadens out behind (*D* in fig. 15 and *P* in fig. 5) to form the rectum or large intestine. *N* in fig. 5 shows the large oval rectal glands, generally three in number. The muscles of the rectum serve to expel the small amount of fecal matter and urine produced by the ant into the cloaca by way of the anus. As fig. 5 shows, the rectum is narrower behind than in front. The anus, which lies near *Q* in fig. 5, leads into the cloaca, like the vagina, the vesicle, etc.

A retrospective glance over the figures and over all that we have just said will amply persuade the reader that social digestion matters a great deal more than individual digestion to our little friends the ants. The individual process scarcely begins before the stomach, the bulb of the gizzard actually answering to our human mouth and gullet, while the ant's mouth is above all a social mouth. If we were great international ants, the universal society of nations would long ago have been formed, and we should have had no world-war!

3 INTERNAL GENITAL APPARATUS

The genital apparatus of ants is very complicated. We can divide it into male and female apparatus. But matters are specially complicated by the fact that the fertilized ♀, after her wedding day, becomes as we have seen a sort of complete hermaphrodite who fertilizes herself, often for years. Now as the worker and the ♃ scarcely ever have this hermaphrodite apparatus, they remain purely female, and are incapable of mating; both ☿ and ♃ can lay eggs by parthenogenesis, as we saw in dealing with ontogenesis. But things are still further complicated by the ergatogynes which we mentioned in connection with polymorphism. These creatures also possess the hermaphrodite apparatus, and are capable of mating. As there are transitions between the ☿ and ergatogynes, we must admit that under exceptional circumstances certain ☿ must be capable of mating. Moreover, we sometimes find in them fairly well-developed rudiments of the hermaphrodite apparatus known as the female seminal vesicle, which we will describe shortly.

I MALE APPARATUS. In the chapter on external anatomy we described the genital valves and their function. We will return once more to fig. 10, where we halted at letter *E*, that is, at the ejaculatory duct. This duct bifurcates at the top, each branch leading to a large pocket *D*, the male seminal vesicle, which must not on any account be confused with the female seminal vesicle which we shall discuss later. Like the latter, it is a reservoir for spermatozoa. Above these, each branch of the canal becomes narrow again, forming the seminal duct marked *C*. Lastly *A* shows the testicles, whose groups of creative spermatozoa are denoted by *B*.

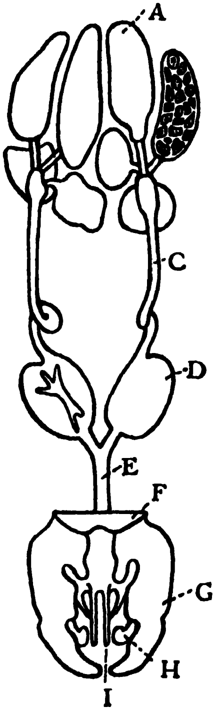


Fig. 10 repeated

Thus the elaborated sperm in the testicles (*A.B.*), like that of human beings, gradually accumulates in the male seminal vesicle (*D*). After copulation, the first stage of which will be seen in fig. 71 (Part III), which represents the marriage flight, the ♂ ejaculates the contents of his seminal vesicle through the ejaculatory duct between the two sagittæ *I*, introduced into the vagina of the ♀. But as the seminal vesicle of the ♀ is more considerable, for good reasons, than that of the ♂, Madame is obliged to have several husbands; she is polyandrous. And that is why the gentlemen of the ant race are never jealous of one another, nor the ladies either, for that matter. Nevertheless, our readers may reassure themselves. Polyandry (polygamy of women) among the ants only lasts a single day, the occasion of their aerial or terrestrial wedding. After that day, the ladies live the lives of recluses, like hermits in their cells.

2 FEMALE APPARATUS. The female apparatus is double, being at the same time ♀ and ♂, at least in the ♀ and the ergatogynes, as we said before.

(a) ♀ apparatus proper. It is represented in fig. 18 in the person of a ☿ of *Leptothorax Emersoni*, which shows a slight transition towards the ergatogyne stage; since it possesses a rudimentary hermaphrodite apparatus (Rec.), side by side with a copulatory pouch (*B.c.*). Here we may also see the tubes of the *ovaries*, ovarioles, three on the right and two on the left, broadened at the base and tapering at the top. They are alternately filled with an egg (*O*) and with the cells *A* which feed this egg.

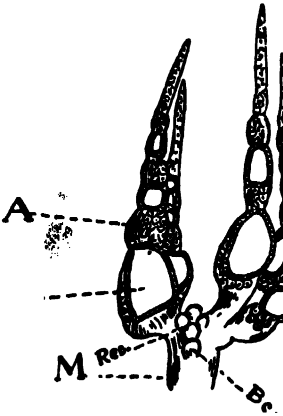


Fig. 18

The number of egg-tubes or ovarioles varies enormously according to genus, species and polymorphism. Miss Holliday has counted 250 in the ♀ *Eciton Schmitti*, and only two in a little ☿ *Cremastogaster*. Miss Bickford found that there were none at all in *Tetramorium caespitum*, though Wheeler considers this doubtful.

The ovarioles, starting on either side from one of the ovaries, lead to an ovarian duct which is at first paired and then joined in the middle to form a single duct, shown in fig. 18 *M*, and fig. 19 *G*. We may call this the *Matrix* or *Uterus*, as Wheeler does, although it has no functional relationship with the uterus of the mammals. This single channel bears on its dorsal surface a *cul de sac* pocket analogous to our human appendix, the source of the dreaded appendicitis. But this *copulatory pouch* has no other purpose than the temporary reception of the semen ejaculated by every ♂. It is shown in *Bc*, fig. 18 and in *H*, fig. 19. The oviducts, uterus and copulatory pouch have strong muscles represented in cross-section in fig. 19.

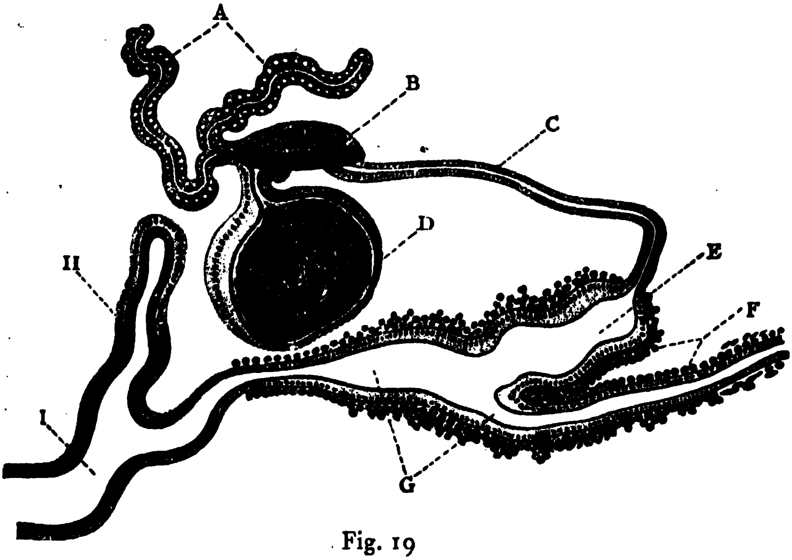


Fig. 19

(b) Hermaphrodite ♀ apparatus. The letter *G* in fig. 19 has two dotted lines, one of which, branching out in the direction of the vagina (*I*) represents the single matrix, while the other, leading towards *F*, represents one of the paired ovarian ducts which are bifurcated in order to reach the ovary. Between these two points diverging from *G*, arises the *seminal receptacle E*, of which we shall speak shortly. We must now return to the copulatory pouch *H*. Near the bottom it leads straight to the vagina (fig. 19, *I*) and thence to a broadened part called the *vulva* which opens into the cloaca.

Surrounded by strong muscles, the *seminal receptacle* of fig. 19 *E* terminates in its upper part by a longish and extremely fine canal, the female seminal canal which connects the uterus with the female seminal vesicle. But in its own upper part, this seminal canal broadens out into a bottle-shaped formation *B*, in order to pour its contents into the seminal vesicle *D*. Provided thus far only with a thin lining (*C*), the seminal canal then broadens out into *B*. Its lining becomes thick and chitinous, and above all is surrounded with very strong muscles (*B*) which may close it when compressed, and which look like a little hood. Lastly, *A* shows a paired accessory gland which pours its secretion into the top of the seminal duct before its entry into the female seminal vesicle. The latter (*D*), varies greatly in size. According to Adam it is 1·5 millimetres long in the queen bee, 1 millimetre in the ♀ *Formica* of the *rufa* group and in *Lasius fuliginosus* ♀, ·7 millimetres in *Lasius emarginatus*, ·6 millimetres in *Tetramorium caespitum*, ·4 millimetres in one *Camponotus*, ·25 millimetres in *Myrmica rubida* and in the ♀ of the humble-bee and hornet. It is plain enough, therefore, that the dimensions are in no way dependent upon the size of the ♀ which possesses them, but solely upon the population of the nest—that is, the supply of sperm which the fertilized ♀ requires for its maintenance.

The next problem to be considered is the way in which the sperm reaches the female seminal vesicle and afterwards flows out to fertilize the eggs laid by the mother ant, which has thus become a secondary hermaphrodite. Alexander Adam, who has studied the question most fully, gives an explanation very similar to that suggested by Emery in connection with the bulb of the gizzard and the pharynx ; he assumes that there is a suction and forcing pump for the sperm as for the honeydew. When the muscles of fig. 19 *B* relax, they parsimoniously allow a few spermatozoa to flow out of the vesicle and fertilize the egg which is to pass through *G;* the muscles of *E* act as a pump, afterwards relaxing in their turn. After copulation, the various circular muscles work in the opposite direction and force the sperm of the copulatory pouch into the female seminal vesicle.

Here lies the explanation of the fact that long life and intelligence are useless in the male ants, and quite the opposite in the ♀.

It likewise explains polyandry on the same principle.

4 Respiration

Like all other insects, ants have no lungs and breathe by *tracheæ*. These are empty ducts which have been ramified and rendered at the same time elastic and open by stiff, microscopic spirals, very clearly shown in various parts (*Q*) of fig. 21. The air flows in and out of the tracheæ by means of the to-and-fro motions of the abdominal segments, moving one against the other as they dilate and contract alternately with the aid of their muscles. They can thus force the air contained in the lungs throughout the whole body, or bring in a fresh supply of air by inspiration. In the winged sexes, a special large tracheal trunk branches off from the strong muscles of the wings which constantly need oxygen in flying. The tracheæ open at the surface of the chitin by way of minute holes, scarcely visible to the naked eye, called *stigmata;* we spoke of them in connection with the external anatomy, particularly when dealing with the epinotum. They are found, however, not only on the epinotum but also on the abdomen, etc. Each of these orifices leads to a short trunk in the interior, provided with a curious valve which serves to close and open it. Behind this valve opens the long ramified tracheal trunk already described. All the ant larvæ possess ten pairs of tracheæ, which are ramified throughout the whole body, and even in certain cells, in order to furnish every part with oxygen (see fig. 13 *K*).

The last fine ramifications cease to have spirals.

5 CIRCULATION, PERITONEUM AND FAT-BODY

Janet and Wheeler are responsible for some excellent studies on the circulation of the blood in ants. Here, as in respiration, everything happens in the same way as in other insects, for in the circulation of the blood, white or red, there is nothing of an intrinsically social character. The blood of insects is white, and permeates the whole interior of their bodies. The heart functions as a forcing and suction pump, causing the blood to circulate in a general way, and not in closed arteries and veins like our own. We have just described the respiratory tracheæ; it is these which circulate the air throughout all the cells of the body, and thus replace to a great extent the circulation of the blood in vessels.

The heart of the ant is situated in the abdomen, above the digestive tube and the stomach, between *L* and *N* in fig. 5, where it is not represented. It is a mid-dorsal tube with five dilatations corresponding to five abdominal segments.

Each is pierced by a pair of lateral openings, provided with valves. The wall of the heart is a simple cuticula with a unicellular matrix (like that of the crop); but it is open at the back, the front and the sides—in the last-named case—by means of lateral valves. The heart is not enveloped by a layer of muscles, but only possesses muscular *fibrillæ* among the matrix cells of its cuticula. The heart is held in its place by numerous suspensory filaments attached to the dorsal chitin of the abdominal segments, as well as to five pairs of transverse muscles called aliform muscles, which are suspended themselves. The aliform muscles are arranged in a fan, whose large central part is attached to each of the dilatations of the heart, above the middle, while each point of the fan is attached to the lateral walls of the abdominal segment. The heart is continued anteriorly by a simple dorsal vessel, slender and non-contractile, called the *aorta*, which crosses the pedicel and the thorax to open into the head. The circulation of the blood begins in the front part of the body, as follows : according to Janet, the aliform muscles contract and draw the heart downwards, so that the suspensory filaments help to dilate it considerably. At the same time the lateral valves open and the white blood fills the heart, which then contracts with the aid of its own fibrillæ and of the relaxation of the aliform muscles ; the lateral valves close and the blood thus propelled flows through the nodes of the pedicel and the thorax in order to spread about the head. Thence, at the next inspiration, it returns to the abdomen by two ways, the dorsal and the ventral sinus, and so the process continues.

In connection with the circulation of the blood, ants have four kinds of cells arranged in little masses in the circulating blood : the pericardial cells, the œnocytes, the fat-cells and the urate cells.. These last no doubt serve to transform the substances which have become valueless and harmful to the blood, in order that they may be transmitted to the Malpighian vessels. The fat-cells are especially abundant in the ♀ after her nuptial flight. They provide her with nourishment during her secluded life after fertilization. The function of the two other kinds of free cells is not clear.

The peritoneum of the ant consists of cells, filaments and cuticulæ, all spread about the abdomen among the various organs we have just described, and the muscles and other apparatus with which we shall soon become acquainted.

In summing up, I will draw the reader's attention to four kinds of forcing and suction pumps present in the ants: 1 the two pumps of the gizzard and pharynx, the one personal and the other social; 2 the sperm-pump, which is social only; 3 the respiratory pump of the abdomen and the tracheæ, which is purely personal; 4 the heart-pump, which is also personal; we human beings have only two pumps, both personal: our lungs and our heart proper—the one that is not sentimental.

6 POISON APPARATUS

This is a very curious apparatus which serves the ant for defence rather than attack—though not always. There are two kinds: 1 The glands of the poison vesicle, with or without a sting; 2 The glands of the anal vesicle.

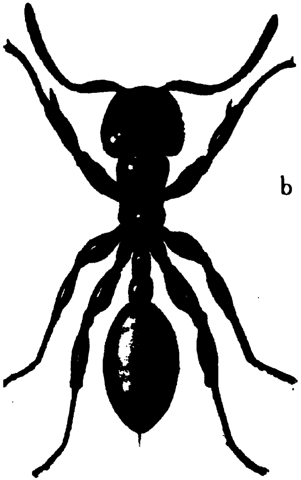
1 GLANDS OF THE POISON VESICLE. These are seen in their natural place in fig. 5, and isolated in fig. 20 and 21. There are two radically different types of poison vesicles, so different that there is no transition between them. It was these that I used, in 1878, as a basis for the division of the old sub-family of *Formicinæ* into the *Camponotinæ* and *Dolichoderinæ*. The poison vesicle of the *Dolichoderinæ* is atrophied and as a rule replaced by the anal vesicle; but it preserves a minute sting, as well as the form it possessed in

a. *Podomyrma abdominalis* Em. var. *pulchra* For. ☿. 10 mm.

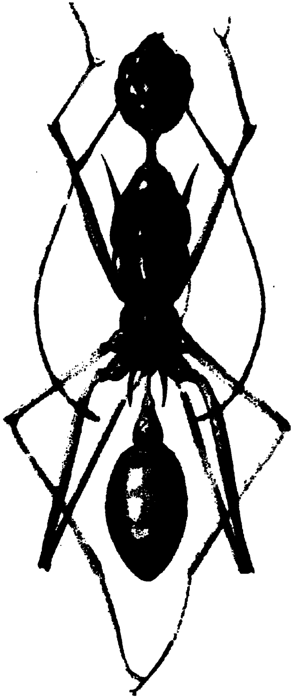
b. *Vollenhovia rufiventris* For. ☿. 6·5 mm.

c. *Aphænogaster* (*Planimyrma*) *Loriai* Em. ☿. 9·5 mm.

a



b



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the other three sub-families. In the *Camponotinæ*, on the other hand, the sting is entirely transformed into a supporting apparatus (fig. 21 *EFG*) for the ejaculatory duct of the vesicle, which also possesses a special cushion instead of the bourrelet of the other type (*CD* fig. 20).

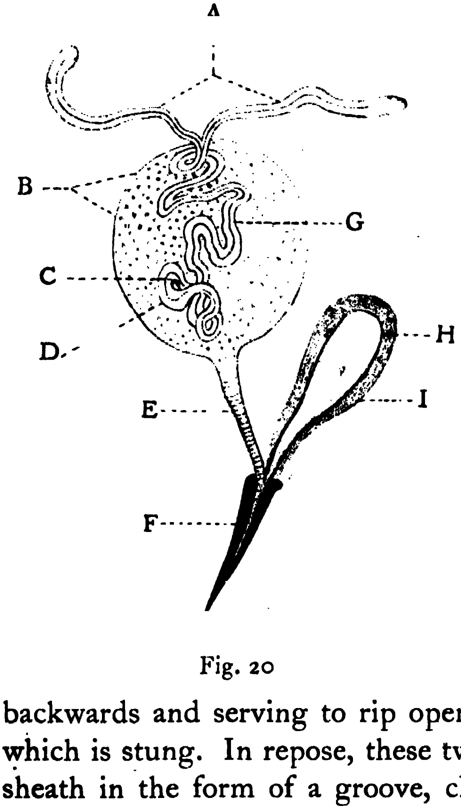


Fig. 20

(a) *Bourreleted vesicle* (fig. 20). In this primitive type, analogous in every respect to that of the Mutillids, wasps and bees, the sting seen in fig. *5 R* and fig. 20 *F* plays the principal. But our figures do not give the details. The sting itself consists of two stylets set one against the other, which in the humble-bee and the honey-bee, for example, are provided with small, oblique, pointed teeth, turned backwards and serving to rip open the flesh of the enemy which is stung. In repose, these two stylets rest in a single sheath in the form of a groove, closed only on the dorsal side and open on the ventral side. The whole is surrounded by two other pointed sheaths, serving as splints. But the two internal points alone are used for pricking. They are continued at their base in the form of two mobile arches which can thrust backwards and forwards their two extremities (the two points themselves) with the aid of two groups of powerful muscles acting in opposite directions, and situated in lateral pairs in the cloaca. When the ant stings, therefore, it advances the two stylets of its sting, which then slide into the groove, and push the two splints aside. At the same time it emits a drop of poison from its vesicle, whose duct to the exterior opens into the distal part of the groove, between the two arches of the points of the sting. Such is the mechanism of an ant's stinging-process.

Now let us deal with the bourreleted vesicle itself (fig. 20). It is spherical, and connected with the sting by a canal which is generally slender and with close transverse folds, as shown at *E*. Strange to say, during the very detailed and careful studies I undertook in 1878, I found it impossible to discover muscles on the vesicle of *Myrmica*, *Pogonomyrmex* and *Dorylus*, while the *Ponerinæ* and various *Cryptocerus* and *Cremastogaster* have a muscular network around their poison vesicles. Can it be, perhaps, that the contraction of the abdomen suffices to expel the poison in the case of our *Myrmica?* The lining of the vesicle is covered with a very thin layer of cells, by which it is secreted.

But the most remarkable thing is the poison-gland itself. It begins at the top of the vesicle, with two free tubes *A*, rounded at the extremity and provided with an outer cuticula covered with fine cells which secrete it, like that of the vesicle. It also has an interior canal, marked in the middle as a simple line (fig. 20), which when greatly enlarged is found to be identical with that of fig. 13 *D*, *A* and *B* (cuticula and its cells), as well as that of *C* (glandular secretion). As in fig. 13, this internal canal is ramified into a host of microscopic canals, each spreading to a single gland-cell, that is, in the protoplasm around its nucleus, as I showed in my earlier work just mentioned. Now all the glandular cells in question lie in the tubes of the gland, between its two cuticulæ, the external one and that of the internal canal.

At the top of the vesicle its two tubes *A* (fig. 20) unite again to form a single one, just as their two little internal canals do. Then a strange thing occurs, which I brought to light in 1878 : the external cuticula of the tubes which are uniting blends with that of the vesicle, while the cells of the gland, the internal canal and its interior cuticula continue their journey to the interior of the vesicle, which they enter in various convolutions (*G* and *D*). This internal part of the gland is therefore suspended right in the middle of the vesicle. At last the gland ends in a button or bourrelet which does not come out well in the figure, enclosing a powerful cluster of cells and resembling the knob of the gizzard, described above and shown in fig. 17. The internal canal opens on the middle of this bourrelet: its cuticula turns upward, like that of the knob in the gizzard, and continues in an external cuticula of the knob, which is nothing more than the internal cuticle of the vesicle invaginated or sheathed in the opposite direction. Thus the poison secreted falls into the midst of the vesicle, owing to the action of the bourrelet and its convolutions, all filled with glandular cells between the two cuticles.

In the *Dolichoderinæ*, the two free tubes of the gland are thicker and the bourrelet is formed immediately after their entry into the vesicle, without any previous meanderings. All the rest is identical, but on a smaller scale and more or less atrophied. Almost exactly the same description applies to certain *Myrmicinæ*, *e.g.*, the *Attini*.

(b) *The pulvinate or cushion-vesicle.* In the *Formicinæ* things are quite different. The sting has disappeared, that is, the supporting apparatus for the vesicle replaces its parts. Fig. 21 *F* shows the left piece, which is the transformation of one of the two sheaths of the sting; *G* shows the transformed groove, *E* the left stylet atrophied and somewhat dislocated in comparison with the original sting, *H* the cloacal membrane, *B* (right) the orifice of the vesicle. This vesicle, which is closed and opened by the muscles of the supporting apparatus (which are likewise a transformation of those of the sting), opens immediately above a broad longitudinal duct. This duct, folded crosswise, is as spacious as that of the bourreleted vesicle is narrow.

The vesicle itself is very large, elongated, and applied to one side of it is a cushion, which is also elongated and which terminates underneath—not at the top—in the two very long free glandular tubes. These resemble the two streamers which young girls used to wear at one time, and which were known as the " Follow me, boys." The structure of the two free tubes is exactly the same as in the bourreleted vesicle ; the numerous ramifications of the internal duct, which reach every gland cell, are also the same, and need not be referred to again. The tracheæ (*Q*), which supply the gland-cells with air, are much more clearly visible. At the lower base of the cushion the two free tubes unite again, and here also their external cuticula adapts itself to that of the vesicle.

But after that the scene changes. The internal duct becomes much larger, and instead of microscopic ramifications each leading to a cell, it provides broad ramifications which are often themselves ramified, but which always end in a cul-de-sac. These constitute the cushion. Between these lies the protoplasm of the gland-cells. These cells also form the matrix of the cuticula of the internal duct and its ramifications. They and their nuclei form polygons at the surface of each ramification. Fig. 21 *R* shows one half of the cushion opened to reveal the mazes of the internal ramified

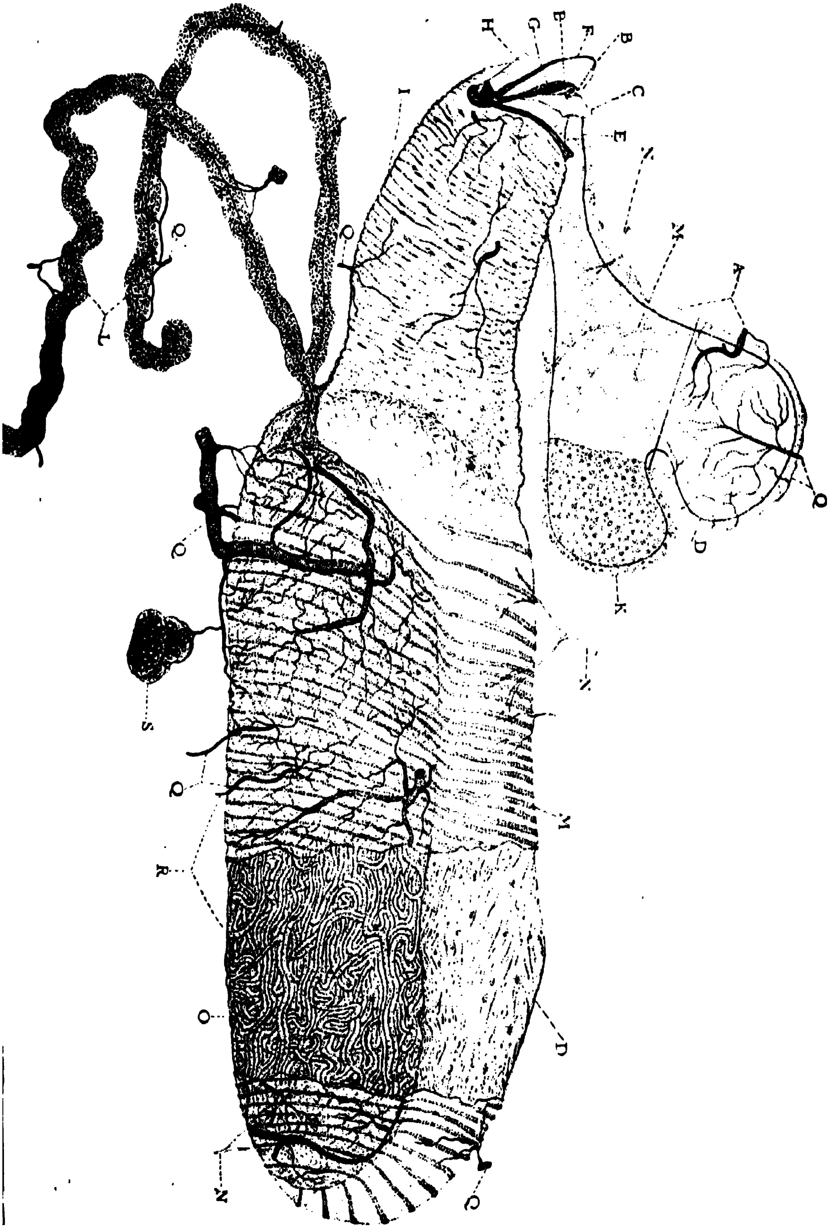


Fig. 21

tube *O*, and one half closed to display the fat-cells and ramified tracheæ (*Q* and *S*). It will be apparent that at the base of the cushion the internal cuticula of the free tubes, instead of sheathing itself in the vesicle, as in the case of the bourreleted vesicle, spreads out considerably under the cushion itself, still separating it from the external cuticula of the vesicle. It does not come into contact with the latter except round the cushion, where the latter ends. The abundance of tracheæ and fat-cells in the cushion are a proof of its importance in the secretion of poison.

On top of all this are elegant muscle-fibres (*M*), regularly spaced, broad on the dilatable portion of the vesicle, but slender where they touch the cushion. When these fibres contract, they ejaculate poison. *N* shows the nerves which cause the muscles to contract. Lastly, *D* shows the external cuticula uplifted from the vesicle to reveal the cells of the matrix and its internal cuticular membrane.

Could you have imagined, dear reader, such a charming apparatus for doing so vile a thing as killing one's fellow-beings by pouring venom into them, either formic acid or some other poison? Yet that is what Divine Nature has done, as will be clearly seen a little later on.

2 ANAL GLANDS AND VESICLES. From the dorsal side of the rectum and the anus come another pair of glands, also finding an outlet in the cloaca through a vesicle which is divided in half at the top. But this is present only in the single sub-family of ants called the *Dolichoderinæ*, which I discovered and described in 1878. Figs. 13 and 22 show its details. *C* in fig. 22 denotes its ring-like orifice into the cloaca, *I* the two sides of the divided vesicle, *N* the network of its muscles, *H* the trachea, *M* the external cuticula, *D* the base common to the two sides of the vesicle.

B shows near the base a kind of funnel with longitudinal folds, which represents the orifice through which the central duct of the left gland opens into the vesicle. *E*, on the right, shows it on its journey. It is obvious at the first glance that the arrangement there is quite different from that of the poison gland. The large spherical cells are shown clustering abundantly like a bunch of grapes, round the solid central duct, which is gracefully upturned before its base. One of them is even in direct communication with it by means of a small but perfectly independent duct. What is the meaning of these large cells? The large stem of the respiratory tracheæ (*H*) appears near the thickest part of the cluster, into which it thrusts its ramifications. Then come the muscles, which branch off from those of the vesicle, reach the bunch of cells and hang like threads ready to be detached. Their purpose may be to press upon each cell and cause the secretion to flow. But we must beware of hypotheses, and content ourselves with stating facts.

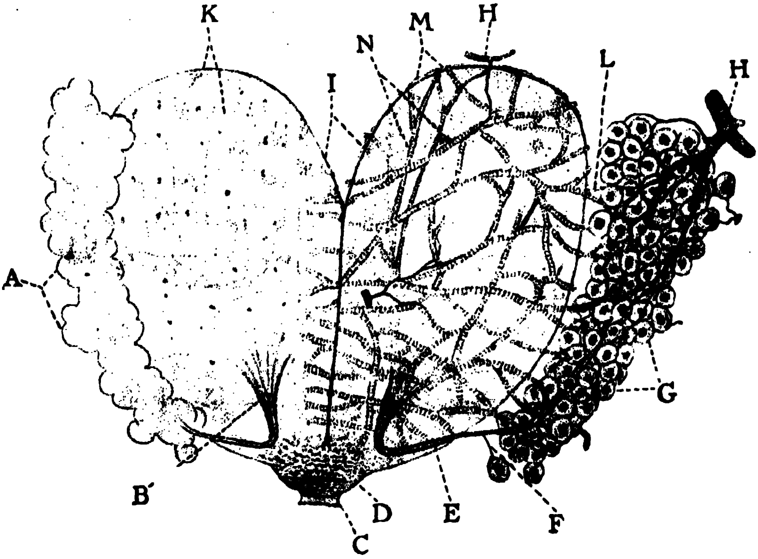


Fig. 22

Let us pass on to the cells themselves (fig. 13), which are amongst the most magnificent phenomena nature reveals to us through the microscope. In connection with the internal central duct of the bourreleted poison vesicle, we have already mentioned the details of the central duct *A*, *B*, *C*, *D*, fig. 13 and in connection with the cuticulæ, those of the branch *E*, *F*, *G*, secreted by a single cuticular cell which entirely surrounds it. This branch journeys to a large single cell *N*, which has its own cuticular membrane corresponding to the external coat of the poison glands and probably secreted by minute cells which I have not been able to discover. Furthermore, a small stem of tracheæ ramifies into four branches (*H*), which penetrate the cell and supply it with oxygen. *H* shows us the enormous nucleus of the glandular cell, that is to say, its membrane, and *I* the numerous corpuscles which occupy the interior of this nucleus. But the most curious thing of all is the fact that the branch of the central duct leading to the large cell, instead of ending there, is prolonged into the interior of its protoplasm between *G* and *O*, where it makes a double circuit and does not come to an end until it has gone through various convolutions between the ramifications of the trachea. The use of a little caustic potash confirmed my belief that the interior circuit of the branch, which was thus prolonged into the cellular protoplasm, alone constituted the chitinous cuticula. The exterior circuit disappeared under the caustic action; it must be in connection with the secretion, and probably corresponds to the secretary vesicles which Meckel describes in dealing with other glands.

So the reader will see that, as the latest efforts of microscopic anatomy have proved a hundred times, the cell of our living tissues is a veritable world in itself, an admirable little chemical factory which varies for each gland and each kind of tissue. It is small in our eyes, as we ourselves are small to the stars and the vault of heaven, but very large to the infinite smallness of vital electrons! But since the ants are relatively very small—the whole *Bothriomyrmex*, which owns the anal gland shown in fig. 13, is scarcely more than 2 millimetres long—and since their cells are nevertheless as large as our own, it follows, as we said at the beginning, that their cells are much fewer in number. Hence their functions are more *individualized*, and we can distinguish each of them and its peculiarities more clearly.

Later on, in Part IV, when we come to deal with their warfare, we shall see what use the ants make of their anal glands and poison glands.

7 Other Glands

I have enlarged upon the description of the two preceding glands in view of their importance in connection with the social habits of the ants; but, with the reader's permission, I will speak more briefly of the others.

The *accessory* gland (*S* fig. 5) is sometimes simple, as in fig. 20 *I*, with its internal cuticula at *H*, sometimes formed in two long tubes, or sometimes simply divided in half, as in fig. 21 *A*. In this figure, *M* shows its muscular network, *N* its nerves, *Q* its tracheæ, *K* the cells which secrete its juice, *D* its cellular coating and cuticulæ, and, lastly, *C* its opening situated immediately under that of the poison vesicle, at the extremity of the cloaca opposite the opening of the anus. The accessory is obviously a gland and a vesicle at the same time, or in other words, a vesicle lined with gland-cells opening into the sting or its transformation.

In contrast to the clear, limpid and aqueous contents of the anal and poison glands, that of the accessory gland is thick, viscous, oily and yellowish. Its use is unknown. It is alkaline, and Janet thinks that its object is to neutralize the acid residue of the poison that has been ejaculated, and thus to protect the surrounding tissues. But it is not easy to explain why the accessory gland is so particularly well-developed in certain ♀, as I have shown. These ♀ do not ejaculate poison. Hence we must be silent and suspend our judgment.

The *labial gland* (fig. 5 *G*) deserves special attention. It is the salivary gland, whose long secretory duct has become single (*X*, fig. 5) and leads to the tongue, under the hypopharynx, between *a* and *b* in the same fig. 5. This duct has a wrinkled cuticle, like that of the tracheæ, situated in the middle of the thorax at *G*, round the œsophagus. The gland itself is large, double (one lies on each side), and composed of several clusters of cells, whose small ducts unite and lead to the central duct, which is single. It is this gland whose saliva moistens the tongue when the ants are licking and tasting food for themselves, for their companions and for their brood, and also when they are cleansing their nymphs, larvæ, cocoons and companions.

The *glands of the pharynx* or vertex (fig. 5 *E*), are glove-shaped ; their function is unknown.

The *mandibular glands* (fig. 5 *D*), are paired and composed of a group of isolated cells.

Each of these cells leads by a little duct of its own to a huge reservoir, situated laterally under each cheek, whose contents are poured out through a broad gap near the base of the mandibles. The reservoir is not shown in our figure. What is the purpose of these mandibular glands? As they are enormously developed in the inflated *Dendrolasius fuliginosus*, which makes a carton nest, I have inferred that their secretion, in this species at any rate, served to stick together wood-rot, and thus to make carton. Other ants may perhaps use them as moistening agents in certain building operations. It seems to me that the carton-building ants—the foreign as well as the European ants—are generally more or less inflated, which argues for the carton-forming function of the mandibular glands.

The maxillary glands (fig. 5 *C*) are smaller and end in front of the mouth. They have cellular ducts forming a bundle on either side of the jaws. Their use is unknown.

The *metathoracic gland* (fig. 5 *I*) is paired. In *Myrmica*, at any rate, the cells lead through their ducts into a reservoir full of air. It is very well developed in *Dendrolasius fuliginosus* and certain foreign ants, *Cremastogaster* of the subgenus *Physocrema*. Its function is not yet known. Janet thinks it gives the nest its special odour, but this is pure hypothesis. I have proved that the penetrating odour of *Dendrolasius fuliginosus* is distributed throughout the head and body.

We have already mentioned the flat, oval *rectal glands* (fig. 5 *N*) in connection with the intestinal canal, as well as the Malpighian urinary canal (*M*). There are still two other sorts of glands, shown as O and Q in fig. 5, but of unknown function. Lastly there are various gland-cells, either scattered or more or less aggregate, in many parts of the body and limbs. We may recall those of fig. 9 *C* to which we have already alluded, whose secretion lubricates the comb of the first segment of the anterior tarsi.

8 NERVOUS SYSTEM

The brain is the organ of the mind, in the ants as in man; but the ants have an instinctively social mind such as we hardly possess at all. In all animals, the brain is the largest and heaviest of the nervous centres. In insects, all these nervous centres have been named 'ganglia.' The first of the ganglia (*F*, fig. 5) lies in the occiput, above the œsophagus; this is the ant's *brain* or supra-œsophageal ganglion. All the ganglia of insects form a chain which corresponds at the same time to our brain and spinal cord. Each ganglion is attached with the one following it by two *connectives*, or cylinders composed of nervous fibres, one on either side. The two connectives starting from the brain attach it, from the two sides of the œsophagus which they surround, to the sub-œsophageal ganglion, which is situated in the middle of the head, between *X* and *F*, fig. 5. It corresponds more or less to our elongated spine. All the other ganglia and their connectives are situated in the thorax and the abdomen.

The ant's nervous system, like that of other insects and also like our own, is composed of *ganglion* cells and nerve fibres. But the fibres do not possess the white, opaque medullary sheath of the vertebrate animals, and are greyish like the cells. Consequently the nerve fibres of insects are confused among themselves, and are distinguishable only in their primitive elements, which are known as fibrillæ. For example, there is a large bundle of microscopic fibrillæ which form the nerve of the antennæ, clearly visible to the naked eye. The *commissures* or *connectives* which unite the ganglia, and which can also be plainly seen, are also only strong bundles of fibrillæ. The ganglia themselves and the sensitive nerve-terminations contain the ganglion cells.

The cells of the motor nerves are found in all the ganglia, for they are centrifugal—that is to say, they send forth their bundles of fibrillæ from the ganglion to the muscles of all parts of the body. Fig. 21 *N* has shown us how the bundles of nerve fibres, which are already ramified, divide into even smaller threads in order to reach every muscular fibre of the poison gland and the accessory gland.

Fig. 23 shows the bundles of fibrils which lead to the terminal organs, that is, to the topochemical ganglion cells of the ant's antennæ. The letter *G* is not well placed : it should extend as far as the swollen spindle which can be seen further on. This spindle is filled with small round nuclei, and is crossed by longitudinal fibrils issuing from the ramifications of the antennary nerve, the nuclei of the swollen part of the spindle are those of the ganglion-cells, whose protoplasm is very indistinctly differentiated, but crossed by fibrillæ. These are again collected at the extremity of the spindle and end in a hollow sensory hair, like that shown especially well in *C*, but also in *B* and *D*. It has been proved that in the same way the nerve fibrils of the human brain enter and cross the ganglion-cells.

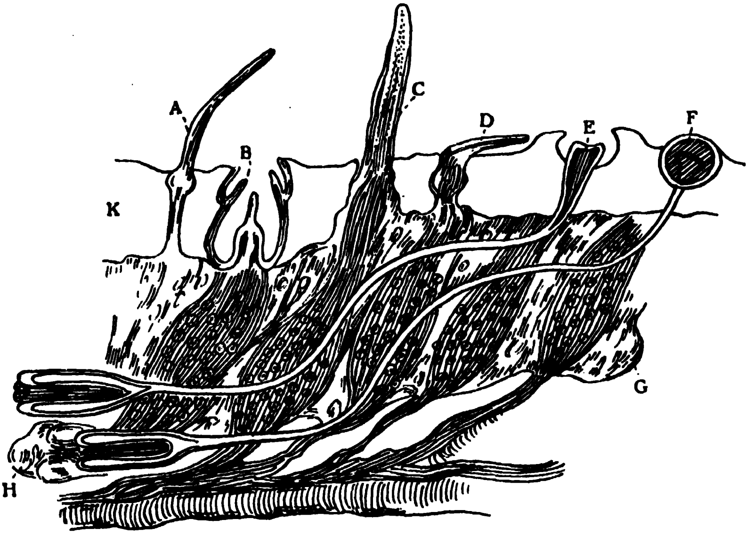


Fig. 23

Apart from the brain the ants have nine ganglia, all bound together by pairs of connectives.

1 The sub-œsophageal ganglion, which innervates the muscles and sensory organs of the mandibles, jaws, tongue, etc., and which is composed of three original larval ganglia fused together by ontogeny; 2 Three ganglia shown in

fig. 5, *Y* and *W*, and belonging to the thorax; they also send out their nerves to the muscles of the legs and wings; 3 A ganglion in the petiole, visible in fig. 5; 4 Four ganglia in the abdomen, including the postpetiole, one of which is marked *U* in fig. 5. The last abdominal ganglion is a fresh combination of three original larval ganglia. They supply the abdominal organs with nerves.

But we must now return to the most important matter—in other words, the brain (fig. 5 *F*). Its details are shown in figs. 24 α and 24 β. Here the nerves of the antennæ, eyes and ocelli terminate. In blind ants, however, it remains as large as in those which are able to see. In 1850 Dujardin discovered the *pedunculate bodies*, shown in fig. 24 *A* (♂ and worker of *Lasius brevicornis*). I have taken these drawings from one of Wheeler's figures, because this author differs from me in the matter of the ant's brain. We see above two grey hemispheres with four white half-moons inside. Each of these is fastened by a peduncle or bundle of grey fibrils (not shown in the figure) to the middle of the central part of the brain, which can be seen ending on both sides in the

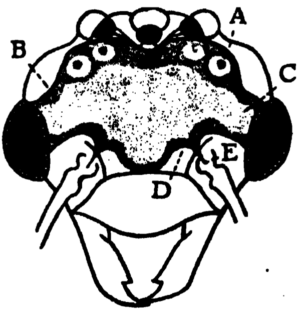


Fig. 24 α

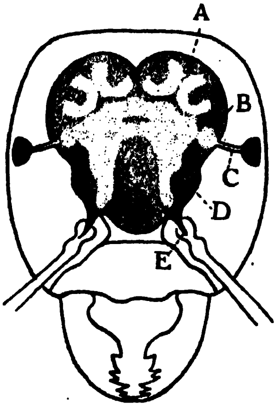


Fig. 24 β

eyes, one of whose facets is marked *C*. The grey cortex is full of very small ganglion cells, while the white half-moons or pedunculate bodies are composed of nerve fibres. Hence this is analogous to our human brain, without being homologous to it in the phylogenetic sense of the word—which I have never declared it to be, for that matter. The cortex is at the periphery: the nervous fibres at the centre.

Nevertheless, in opposition to Wheeler, I have good reasons for holding to my opinion of 1874, which was already shared by Dujardin and Leydig, and which Rabl-Rückhardt upheld in 1875, namely, that the pedunculate bodies are the great brain of the ant. I do so for imperative reasons which Wheeler does not sufficiently consider :—

1 The destruction of the pedunculate bodies immediately deprives the ants of their intelligence, their memory, and the general direction of their instinctive actions, as is the case with fishes deprived of their middle brain, which is their most important centre; though it is not phylogenetically homologous to the cerebrum of man and the mammals. I have proved these facts by numerous irrefutable experiments upon living ants.

2 The development of the pedunculate bodies, which are very large in blind ants, is absolutely independent of that of the sense-organs, particularly therefore of the eyes, as well as that of the muscles. It depends all the more, in the ants, on the development of the intelligence.

3 Because I have said that the brain of the ♀ is proportionately smaller, as a rule, than that of the ☿, Wheeler thinks that I regard this ♀ as a degenerate being. That is quite wrong. I recognize, as he does, that we should not generalize and that the brain of certain ♀ may be equal to that of the worker, even in the matter of proportions. Still, this is distinctly the exception, for as a rule the instincts

and intelligence of the ☿ surpass those of the ♀. I also recognize that the ♂ do not *always* possess such atrophied brains as I formerly believed. Neither are the ♂ equally stupid in all species and genera; their instincts vary. But in my opinion Wheeler has drawn their brain too large in the case of *F. fusca*.

Wheeler believes that he can interpret the great development of the pedunculate bodies in the ☿ in general—and he does not deny this development—by the fact that the worker is a ♀ arrested in its development, so to speak, and that the brains of the young animals in general are proportionately better developed than those of the adults. Here, I consider, Wheeler is guilty of regrettable confusion. All that he says is true for the mammals, birds, etc., for in their case, as in ours, the mind-brain develops during childhood and adolescence and afterwards tends to crystallize. But the insects are entirely different. The brain of the larva is altogether inferior, and it is this alone which grows. The brain of the adult is therefore completely prepared and preformed during the metamorphoses from the stage of the adult larva to that of the nymph: but it does not *begin to work* until the phase of the complete adult ant is reached. Hence the transformation of the ♀ into the ☿ in the phylogeny of ants has nothing in common with the psychic activity in the youth of a mammal. The transformation in question is adapted by phylogeny to the social needs of the community, which usually demand a great deal of intelligence on the part of the ☿, a little less on the part of the ♀ and, with some special exceptions, very little on the part of the ♂.

And so I stand fast by the view I expressed in 1874 in my *Fourmis de la Suisse*, namely, that the pedunculate bodies and their cortex are certainly the great brain of the ants ; it may be otherwise with the king crab cited by Wheeler, with which I am not acquainted.

Above the pedunculate bodies in fig. 24 α, we see *three ocelli* and their *nerves*, but the nerves evidently travel directly through the pedunculate bodies to the *middle brain*, which is situated underneath. In fact, where there are no ocelli (fig. 24 β), the pedunculate bodies are all the better developed. Through the optical lobe *B* (figs. 24 α and β) which is a special lateral swelling of the middle brain, the latter communicates with the optic nerve *C*, whose structure is very peculiar and which extends to the facetted eyes.

In front of the brain (D figs. 24 α and β) we see the olfactory nerve, which consists of large ganglion cells, while *E* shows the nerve which extends to the antennæ. Beneath the olfactory lobe is a small brain lobe which sends out the other nerves to the labrum and pharynx.

Apart from their ganglia, which represent, as we said before, the brain and the spine, the ants have other small ganglia corresponding to what is known as our *sympathetic* nervous system, as well as the nerves arising from them, which continue to the intestinal canal, above and below.

9 SPECIAL SENSES

1 EYES. Ants have two kinds of eyes : the facetted eyes (fig. 6 *C*), and the simple eyes or ocelli (fig. 6 *D*). But phylogeny proves that the facetted eye is derived from a conglomeration of simple eyes transformed. Hence the simple eye is primitive. When the ocelli exist, they are three in number and are situated on the vertex, the front one being in the middle. The genus *Eciton* proves the transition, however, for its ordinary lateral eyes, instead of having facets, are transformed into ocelli again.

(a) *Ocelli.* The ocelli, shown in fig. 24α, *A*, are very large in many of the ♂, and may become very small in the apterous sexes, finally disappearing. They have a single, rounded cornea beneath which we see the black mass of the pigment. The cornea represents the external chitinous cuticle of the ocellus, which has become transparent. Other transparent bodies underneath (crystalline cone and vitreous body) are all likewise cuticular but surrounded by a black pigment which concentrates the light received by the cornea upon the retina situated at the back of the eye. The large ocelli contain a considerable number of visual nerve cells, while the small ones have only one or two, more or less atrophied. But as the ocellus is immobile, it cannot enable the ant to perceive objects; it can only determine the general direction of the light, and I believe that it serves principally for near vision.

It is directly derived from the primitive eye by phylogeny.

(b) *The facetted eye.* We owe the discovery of mosaic sight to Müller. Attempts have been made to invalidate his theory, but Grenacher and Exner have definitely proved it; we shall have more to say about it later. Here we need only remark that the facetted eye can only see the single image of an object directly, not reversed by a crystalline cone, as in our own case. It does not see as many images as there are facets, as some people have claimed. Every facet has a convex cornea and underneath it, in succession, what is known as a crystalline cone, a vitreous body, and a rod, all more or less cylindrical and composed of four transparent cells of a modified and transformed cuticle. The four cells thus unified are surrounded by a black pigment, and rest at the bottom upon the ganglion cells of the retina. Owing to the pigment, which isolates it, each facet receives only a single ray of light. But on account of the convexity of the eyes, the light strikes them from various directions.

The more facets an eye possesses, the more do the rays of light which it receives *differ in colour and intensity*, according to the objects which reflect them. Thus an insect possessing very convex eyes with many facets can see fairly distinctly the outlines of objects which are not too far away. But Exner has furthermore proved that the facetted eye chiefly sees *moving things*, and therefore sees best during flight. *When the insect itself and the objects are all motionless, the insect scarcely sees for more than a few moments;* attentive observation of insects suffices to confirm the fact, especially if a little experimental work be added.

A flat eye with a small number of facets, therefore, can only see very indistinctly, even when the insect is moving; all careful study confirms this. When an ant remains motionless for a few moments, it no longer has any visual perception of objects which are not moving. It is different in our own case, since: 1 Our eyes themselves are mobile; 2 By closing the lid we renew the sensibility of the retina every moment; 3 Our crystalline lens brings about the convergence and concentration of the luminous rays given out by objects, at the same time turning them upside down; thus it projects distinct images upon our retina.

Thus according to the convexity of the eye and the number of the facets, the retina of insects, including ants, receives a more or less distinct image of an object; but the image is modified during movement. This, dear reader, is the fundamental fact you need to remember. And this is why, in general, the winged sexes among the ants have large convex eyes with many facets, as well as ocelli—especially the ♂ which need to overtake the ♀ in the air with great precision—whereas the apterous sexes usually have only small, flat eyes, and are sometimes even blind. Here, as in many cases, the exceptions confirm the rule: that is to say, they can be explained by the type of life.

The retina of ants ends in a very complicated and extremely interesting network of nerves which may be called the optic nerve (*C* figs. 24 α and β) and which reaches the optic lobe of the brain in *B*.

2 SMELL. The ant's nose is situated in its antennæ, not right at the bottom of the nostrils, like our own. Hence it is mobile, and turns outwards, and it can touch and probe the objects it perceives, as I proved clearly in 1886 and afterwards. In connection with brain we have already spoken of the olfactory lobe, the nerve of the antennæ and their terminal *topochemical* organs (fig. 23, *C*, *D* and *B*). By topochemical I mean a sense of smell which informs the ant as to the topography of the places surrounding it by means of chemical emanations, which give an odour to objects.

I have distinguished two types of these organs in ants, the olfactory *clubs* and *plates* (*B*). Both are hairs, modified and hollowed, reached by the terminations of the olfactory fibrillæ, as indicated above. At *C* can be seen how the external club-like cuticle of the skin grows constantly thinner, in order to perceive odours better. The appressed plates are quite oval and transformed in the bees and in some ants; and in the ants they show all the transitions to upright clubs in the intermediate form of oblique hairs (see *D*). Here it is often the middle part which thins out, rather than the extremity. *B* shows how the hair gradually falls back again into the chitin inside. Olfactory plates and clubs are especially abundant in the club of the antennæ, chiefly on its last joint. In point of number and clearness both are in direct relation to the development of the topochemical sense of smell. The base of the funicle has only a very few plates and clubs and the scape has none.

3 TOUCH. *A* in the same fig. 23 shows one of the numerous *tactile hairs* which are actually spread over the whole body,

though very unequally. They are distinguished from ordinary pilosity, which we have seen to be very variable, by the fact that they are also hollow and that a small nerve penetrates to their interior. For the rest, all the true upright hairs are movably articulated to the chitinous integument, in contrast to the prickles and spines. The sensillæ show all manner of varieties, whose functions are not clearly understood: for instance, certain hairs may disappear. But with these we are not concerned.

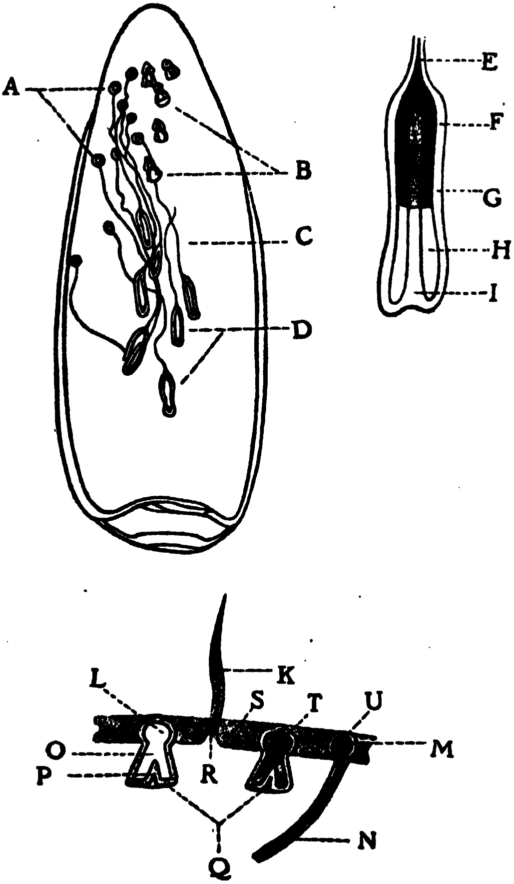
4 TASTE. In connection with the tongue and jaws we have already mentioned the gustatory papillæ, provided with nerves. We shall not deal with them again: I need only refer to figs. 4 β and γ, *M* and *O*.

The function of all the other sensory organs found in the ants are obscure; these organs are as follows:

5 CHAMPAGNE-CORK ORGANS. These are represented in figs. 25 α and γ, *B*, *T* and *L*. Their name indicates their form. They are found scattered over the various funicular segments of the antennæ. I was the first to discover and name them. Each of them consists of a double hair, often full of air and sunken into the chitinous cuticle. Fig. γ (L) shows a champagne-cork filled (*O*) with some kind of liquid, *T* shows another full of air, and *Q* the internal hair. Whether there is a nerve or a gland underneath this hair, no one has hitherto been able to ascertain, but I feel that it must be a sensory organ. It is the same with the following curious organs:

6 FLASK-SHAPED ORGANS. These are shown in figs. 25 α and γ *A*, *C*, *D*, *M*, *N*, *U*. Fig. β gives their detail. Hicks was the first to discover them. They are brought about when the external chitin of a hair becomes invaginated lengthways inside a funicular joint of the antenna. This invaginated hair opens in *U*, almost level

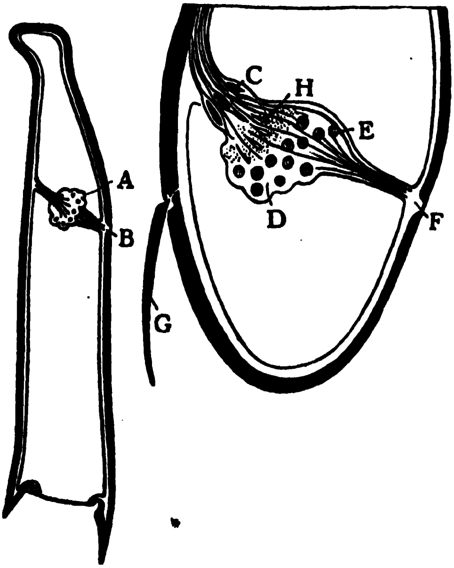
with the surface of the antenna, as indicated in *F* and *E* fig. 23 (Wheeler). Thence it continues in *U* (fig. 25 γ) through a long, narrow canal *N* (fig. 25 γ) and *C* (fig. α) to



Figs. 25, α, β and γ

end in *D* (fig. α) or *H* (fig. 23). It is still doubtful whether the object seen in *H* (fig. 23) is a gland, as Wheeler thinks, or a nerve, as I prefer to think. I, like Wheeler, have seen the thing itself, but I have not been able to decide. Whatever it may be, the ‘ flask ’ *D* and its canal *C* (fig. 25 α) are just as frequently full of air as of liquid. Fig. 25 β shows an isolated flask half-filled with air, *E* being its exit-duct full of air. *F* shows the internal hair surrounded with air, *I* its base surrounded with liquid, *H* the liquid, and *G* the chitinous cuticle of the ‘external’ hair which has relapsed and been invaginated in the interior. The flask therefore contains a hair inside. The flasks, like the champagne-cork organs, are spread over the funicles in all ants, irrespective of the development of the sense of smell or sight. With regard to their phylogeny, I ask the reader to compare them with the relapsed hair *B*, fig. 23.

7 CHORDOTONAL ORGANS. These were detected in the tibiæ by Lubbock in 1877, and represented in fig. 26 α and in oblique section in 26 β. They bear such a close resemblance to the much better developed organs of the cricket and grasshopper that they too would seem to serve some purpose connected with hearing. But this auditory function cannot be proved in the case of the ant. Janet also found chordotonal organs in the head and thorax. Each consists of a spindle-shaped bundle containing a gland with cells to secrete the chitin. The gland is combined



Figs. 26, α and β

with the ganglionary cells of a nerve. Fig. 26 α is a longitudinal section of the tibia of *Myrmica rubra* ; *A* shows the chordotonal organ and *B* the fossa through which it makes an exit. Fig. 26 β, a cross-section, shows the chordotonal organ *D* and its fossa *F*, its special cells *H* known as the scolopal bodies, its ganglion cells *C* and the nerves which arises from them, and the nucleus *E* and *D* of the chordotonal cells. Whatever this structure may be, it is certainly an organ concerned with sensory nervous activity. The presence of the nerve proves this.

8 JOHNSTONIAN ORGAN AND OTHERS. Johnston (1855), Child (1894), Berlese and others have described various other sense-organs which other insects possess and which Wheeler thinks are also present in the ants. Possibly they may serve for different varieties of touch, hearing or other forms of sensibility, but we cannot be sure and had better leave the matter in abeyance.

10 MUSCLES

In dealing with other organs in the ant's body, we have already spoken of various muscles. There are two kinds of muscles, the striated muscles used in rapid movements and the smooth muscles used in slow movements—like those of our intestines, for example. Striated muscles only are found in the ants. They are composed of filaments, each with a long cell consisting of a fibre split up into small, contractile elements alternating between microscopic greyish rectangles and other little rectangles which are clearer. This may be seen in fig. 12, *B* and *G*. The same thing can be observed in the large muscles of the head, thorax and abdomen, in figs. 27 and 28. When a muscle contracts, the little rectangles are drawn near to each other under the irritant influence of the nerves; when they relax, the little rectangles are drawn apart again.

Fig. 27

These are nerve electrons, once christened by me 'neurocymes' (nerve waves), which irritate the muscles. We see that a muscular fibre of the bulb of the gizzard in *Bothriomyrmex* (fig. 12 *B*) has no more than five pairs of small elementary rectangles used in contraction. Here it is easy to realize that the cellular elements of little insects come very near to being special organs in their entirety!

Fig. 27 shows the musculature of the thorax, the scale, and the abdomen of a ☿ *Lasius*, after Nasonov. The attachments of the muscles are visible, and the reader can almost see how each muscle as it contracts moves the rings of the abdomen against one another, the whole

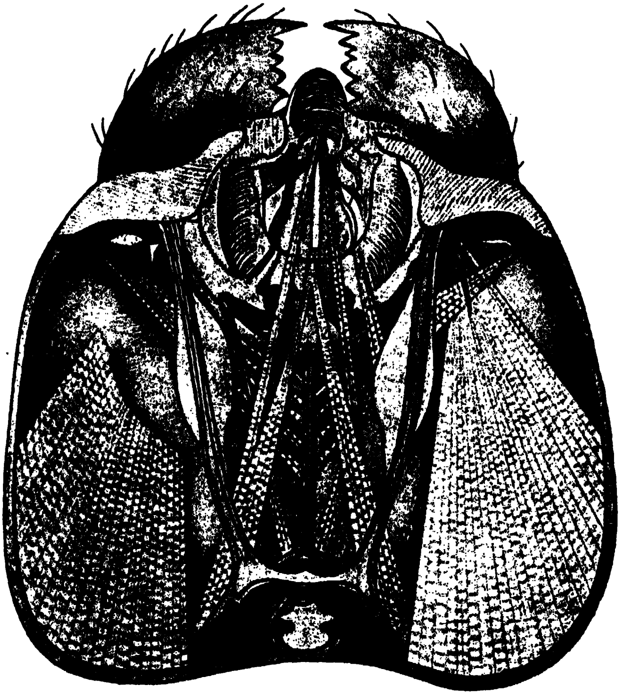


Fig. 28

abdomen against the shell of the petiole, the petiole against the metasternum, the head against the prosternum, etc.

Fig. 28 shows the enormous muscles which close the mandibles and the manner in which they are attached to them ; it also shows the long muscles of the tongue, etc. In fig. 9 *A*, and more particularly in fig. 8, we saw the muscles of the legs. It seems unnecessary for me to go into further details. In the figures indicated anyone can see how the ant's brain sets the outside muscles working, and it has already been shown in connection with the gizzard and the heart, for instance, how it sets them working inside.

Before closing the section on the anatomy of the ant I must apologize for not having dealt with that of their larvæ and nymphs. But that would have enticed me too far afield—besides, this anatomy is as yet imperfectly understood. Furthermore, we have said all that is necessary in this respect while dealing with phylogeny and ontogeny. It is an anatomy of organs intended for purely individual service, devoted primarily to digestion, and it has to be entirely transformed in the nymph in view of the social services which the adult ant must render. It is these services which concern us here: it is not my intention to provide a course in embryology. Those who desire such a thing may consult the works of Janet on the ontogeny of the insect (1909) or of Wheeler (*Ants*, 1910).

For this reason, too, I have thought it desirable to spend all the more time on the anatomy of the adult ant, since this constitutes the foundation on which its habits have developed. And these habits themselves have gradually transformed the anatomy which the ant possesses as a social being, according to the special details of its numerous species, races and varieties, which we are now about to discuss. Conversely, social measures have rendered the larva more and more dependent upon the adult ant, and this has brought about retrogression in its anatomy in all those respects which rendered its ancestors relatively independent of the adult insect, like the caterpillar or the larva of *Tenthredo*, for example. The larva of the higher ants is scarcely more than a receptacle for swallowing what is regurgitated into it, digesting it, and growing.

Chapter V

CLASSIFICATION

Rest assured, dear reader, that I shall not confront you with an arid and erudite system of classification in connection with my little friends—which will become yours too, I hope. I only wish to help you to extricate yourself from the maze of their species; and you have already had an opportunity of discovering that it is impossible to do this without giving them names. As the people of every country name them differently, we must perforce keep to the Latin names, the only ones which are fixed and uniform throughout the world. Since the time of Linnaeus, each species has possessed two names, that of the genus—the group name, which comes first—and that of the species, which comes second. Thus *Messor barbarus* L. means genus *Messor* Forel, species *barbarus* Linnaeus, for in science we always add the name of the author who was the first to describe the animal in question; but in future I will spare you these authors' names. If an author re-describes, under another name, a species which has already been described before his time, he is punished by having his new name attached as a synonym. Thus *Formica Berthoudi* Forel is a synonym for *Plagiolepis custodiens* Smith. A punishment like this is as wholesome as it is efficacious.

But since Linnaeus made his classification things have become much more complicated, owing to the enormous multiplication of species. To avoid this tangle, we have multiplied the genera, and have often divided them into sub-genera. Species which are closely akin and between which there are transitions are divided into *races* or *sub-species*, and the latter are often divided into *varieties*, still more like each other and more transitional. I accept as genuine species only those which do not produce fertile offspring among themselves. Thus the following example shows the maximum complication of names, the sub-genera being in parenthesis, according to practice:

Genus *Formica* L. (the abbreviation adopted for the name of Linnæus) *s.g.*—the abbreviation for sub-genus—(*Serviformica* Forel) *fusca* L.r. (the abbreviation for the race), *glebaria* Nyl. (the abbreviation for the author) Nylander, v. (the abbreviation for variety), *rubescens* Forel. So we can summarize this as follows: *Formica* (*Serviformica*) *fusca* L.r. *glebaria* Nyl. v. *rubescens* For. The authors responsible for the genera and sub-genera are left out, it is true, when we name the species, races and varieties. But in this book I will permit myself to abbreviate still further, not only by leaving out the authors' names, as I have hitherto done, but often even by replacing the name of the genus by that of the sub-genus, and saying *Dendrolasius fuliginosus*, for example, instead of *Lasius* (*Dendrolasius*) *fuliginosus*.

In addition to all this, the *sub-families* have been divided into *sections*, these sections into *tribes*, and some tribes even into *sub-tribes*—all in order to account for more than 7,500 species, races and varieties of ants known to-day, that is, to account for as much of their phylogeny as possible.

In fact, the tendency of the present-day classification of living beings is to establish as far as possible their true phylogeny. Now this is no easy matter. If we wish to make the slightest headway with it, we make use of every scrap of evidence. 1 Here we at once think of external and internal anatomy, in their minutest details. And it is the constancy of characters which always turns the balance in favour of a higher grade of classification. When this constancy is great and as absolute as possible, it wins the day. 2 The same applies to habits, which are scarcely less important. The structure of the nests is included among habits, and is very valuable evidence. But there are small details of habit which are often characteristic of a species—such as continuous or fitful travelling, the choice of night or day for the nuptial flight, a more or less subterranean mode of life, etc., etc. The cultivation of fungi, for example, is characteristic of a whole tribe, the *Attini*. 3 Ontogeny sometimes supplies important specific characters: the structure of their larvæ and their habits, the manner in which the nymph is formed —with or without aid, with or without a cocoon, etc. 4 The degree of polymorphism in the ♀ or the ♂, described above. 5 The parasitism of other species, and their symbiosis (mutual dependence) with certain plants, etc. All these facts must be utilized if our classification is to be neither artificial nor dogmatic, but simply natural.

None the less, the insufficiency of our knowledge often compels us to make divisions which are very doubtful, and sometimes even deliberately artificial. For example, consider the cosmopolitan genus *Camponotus*. Linnæus, Fabricius, Latreille, Smith, Roger, Mayr, Emery, Wheeler, Santschi, myself and many others have described between us more than a hundred species, races and varieties of this genus, but in the end we find it beyond our present comprehension! So what are we to do? To cut the Gordian knot, I have taken my courage in both hands, playing an unusual trick with phylogeny and dividing this very homogeneous genus *Camponotus* into twenty-five more or less artificial sub-genera, based for the most part upon those external characters known as characters of convergence. By way of excusing my misdeed, I have owned it quite frankly from the very first, which is wiser than trying to hide it. My perspicacious colleagues would have recognized it immediately, all the same. I therefore forestalled them, on the excellent lines prescribed by the German Busch in his *Selbstkritik* (Self-criticism), which I recommend everyone to read, and which I have translated into French rhymes in a little pamphlet *La morale en soi.*

On the other hand, internal anatomy enabled me, as I have said, to divide the old sub-family of *Formicinæ* into two very natural and distinct sub-families, the *Camponotinæ** and *Dolichoderinæ*, by reason of their poison apparatus. The gizzard furnishes very good characteristics for tribes, etc., etc.

At present we divide the family of *Formicidæ* (the ants) into five sub-families. These are the characters of the first three, according to Emery:

1 PONERINÆ. Postpetiole differentiated by a more or less noteworthy constriction of the following segment (except the tribe of *Odontomachini* and a few males of the *Ponerini*), nearly always as large as the segment in question (except *Myrmecia* and a few *Prodorylinæ*). Consequently it is doubtful whether the abdomen should include the postpetiolar segment or not. ☿ and ♀ armed with a powerful sting.

A stridulatory organ usually developed in the anterior and dorsal articular surface of the segment following the postpetiole; this organ consists of very fine tranversal striæ on the articular surface.

Medial spur pectinated, when present, with the exception of the legs of the last pair in a small number of genera; simple lateral spur.

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* The present *Formicinæ*. See p. 134 (5).

Dimorphism of the workers ill-defined: females usually differ but little from the workers. There are ergatoid females (ergatogynes) in several genera; they display almost the same structure of petiole and postpetiole as the worker; by way of exception, the female of *Acanthostichus quadratus* Emery possesses characteristics similar to those of the ♀ of *Dorylinæ*.

Anterior wing with typically two closed cubital cells; the aberrant genera are an exception.

The ♂ of a small number of *Ponerinæ* which show no limiting constriction at the back of the postpetiole belong to the section of the *Euponerinæ*; they differ from the ♂ of the sub-family of *Dolichoderinæ* in the poor development of their mandibles. For the ergatoid apterous ♂ of *Ponera*, see this genus.

Nymphs enclosed in cocoons.

As a rule the *Ponerinæ* do not constitute large societies; there are exceptions to this rule, however, as I shall mention when dealing with the habits of certain genera (*Myrmecia*, *Leptogenys*).

Wheeler says that these ants have not the same faculty of regurgitating the juices accumulated in the crop as is possessed, for example, by *Formica*, *Campanotus* and *Myrmica*. They feed their larvæ directly by bringing them pieces of insects or some other food, which the larvæ have to gnaw for themselves.

The *Ponerinæ* therefore supply food direct to their larvæ by a more primitive process, exceptional among the other ants.

The larvæ of the *Ponerinæ* are remarkably mobile for ant-larvæ. When they are disturbed, they move their long necks as though trying to defend themselves. Many of them have tubercles on the skin. (Fig. 1 *A*).

The nymphs are enveloped in a very resistant cocoon, which is generally brownish in colour. They can tear this cocoon apart and free themselves, without the aid of the workers.

2 DORYLINÆ ☿ and ♃. Epistoma nearly always very short, and not bounded by any suture.

Frontal carinæ vertical, not covering the insertion of the antennæ. Antennæ, often consisting of less than twelve joints, inserted near the mouth and quite near one another.

Palpi with three joints at most, sometimes (*Leptanilla*) one joint.

Sutures of the thorax more or less effaced ; mesonotum touches the epinotum at the back, leaving no room for the metanotum.

Spurs pectinated, when they are not rudimentary.

Postpetiolar segment not separated from the following segment by a constriction in all the genera; in *Eciton*, *Ænictus* and *Leptanilla*, on the contrary, it is narrow, representing the second joint of a pedicel consisting of two abdominal joints.

Spur well-developed.

♀. Apterous; differing considerably from the worker in the form of the head, as well as in that of the petiole and postpetiole.

Epistoma like that of the worker.

Frontal carinæ more or less apart.

Antennæ ten to twelve-jointed.

Ocelli absent; eyes no further developed than those of the worker; ♀ is blind when the ☿ is.

Segmentation of the thorax relatively reduced; no trace of wings, or with a rudimental wing-insertion (*Dorylus*).

The postpetiole is not separated from the following segment, even in those genera in which the pedicel of the worker's abdomen consists of two joints.

Abdomen very long and voluminous.

♂. Epistoma and frontal carinæ almost like those of the ♀. Mandibles well-developed; generally large; very short in *Leptanilla;* much longer in the other genera.

Highly developed eyes, and ocelli.

Thorax normally segmented, bearing wings.

Conditions of the petiole and postpetiole almost the same as in the ♀.

Genitalia completely retractile (*Dorylini*, *Ecitini*) or exserted and non-retractile (*Leptanilla*); sub-genital plate split or furcate: cerci lacking.

Larvæ more or less cylindrical, with short hairs, and no hooked hairs.

Nymphs naked (*Dorylus*, *Eciton*), or enclosed in cocoons, *Eciton Burchelli* (after W. Müller).

P.S. Lastly and chiefly: habits exclusively nomadic (Forel).

3 Dolichoderinæ. ☿. Generally monomorphous, or under exceptional circumstances more or less dimorphous (a few *Azteca*).

Epistoma prolonged between the frontal carinæ (*i.e.*, between the joints of the antennæ); frontal area more or less distinct.

Palpi usually have the typical number of joints, maxillaries six-jointed, labials four-jointed.

Twelve-jointed antennæ, except in the genus *Semonius*.

Metanotum takes part in forming the dorsal surface of the thorax; the stigmata of this segment often project over the back.

Pedicel consists of one segment, *i.e.*, is formed from the petiole alone, the postpetiolar segment of the abdomen constituting the basal segment of the abdomen. There is no striated surface performing the office of stridulatory organ between the postpetiolar segment and the one following.

Cloacal orifice with transverse slit, as in the Formicidæ with stings, usually at the ventral surface of the abdomen so that the fourth segment terminates its dorsal surface; but sometimes, as in genus *Technomyrmex* and some *Tapinoma*, the fifth segment is longer than the fourth and its dorsal lamella (dorsal valve or lip of the cloaca) becomes apparent when the abdomen is viewed from above.

Sting rudimentary, except in the genus *Aneuretus*, where it is well-developed and may project.

Spurs of the middle and posterior tibiæ pectinated; this spur corresponds to the medial spurs of the *Ponerinæ;* sometimes a second lateral spur, simple and smaller, can be distinguished.

♀. Always winged; otherwise like the worker, except for the eyes and ocelli and the form of the thorax, etc., which have the characteristics common to the winged and fertile forms.

For the wings, see the characters of the male.

♂. Epistoma more or less prolonged between the frontal carinæ.

Mandibles like those of the worker, or else short and narrow; palpi like those of the worker.

Antennæ thirteen-jointed (the male of the genus *Semonius* is unknown); usually the scape is no longer than the second joint of the funicle, but in some genera it is much longer (*e.g.*, *Tapinoma*).

Petiole and postpetiolar segment as in the worker and female; similarly with the spur.

Neuration of wings very variable. In some genera there is a considerable difference between the wings of the sexes, the males having a reduced neuration (*Dorymyrmex*, *Forelius*, *Iridomyrmex*).

The males of the *Dolichoderinæ*, which have two closed cubital cells, are distinguished from those of the *Euponerinæ*, whose postpetioles are not separated from the abdomen by a structure, because their mandibles are well-developed. Those which have long scapes and wings of the *Formica* type can be distinguished from the males of the *Formicinæ* by the epistoma, which is prolonged beyond the frontal carinæ.

Nymphs consistently deprived of cocoons; larvæ generally immobile.

The sting, poison-gland and bourreleted poison vesicle have almost the same structure as in the *Dorylinæ*, *Ponerinæ* and *Myrmicinæ*, but they are more or less rudimentary; the genus *Aneuretus* is an exception, and has a well-developed sting. In the *Formicinæ*, on the other hand, these organs have a totally different structure.

Furthermore, the workers and females of the sub-family *Dolichoderinæ* possess a pair of anal vesicles into which the unicellular anal glands pour their secretion. Most of the ants of this sub-family, when they are irritated, *e.g.*, in warfare, emit the contents of their anal vesicles from the opening of the cloaca (see fig. 97, Part IV). On coming into contact with the air, this matter becomes resinous and adheres to the tegument of other insects. As the ants expel the secretion of these vesicles, the observer perceives a peculiar aromatic odour, which I have called "the Tapinoma odour." In fact the abdomen of a *Tapinoma* has only to be pressed between the fingers, and this odour will be noticed. There are *Dolichoderinæ* which have not the odour of *Tapinoma;* the secretion of the anal vesicles does not become resinous (*Bothriomyrmex* ☿ and most of the *Dolichoderus*).

Next we come to the characteristics of the other subfamilies according to Emery.

4 Myrmicinæ. In all the sexes, the pedicel *always* has two little nodes, greatly constricted (fig. 5); the petiole and postpetiole. The gizzard is simple, as in the *Ponerinæ*, except that of a few *Cryptocerini*, which has a large chitinous bulb in front, projecting into the crop.

The sting of the ☿, ♀ and ♃ varies, and may be almost completely atrophied; but the vesicle is always bourreleted. A stridulatory organ sometimes exists, but it is also frequently lacking. In a few parasitic genera the worker may disappear; when she is present, her dimorphism can be very great, with or without distinct ♃, or else absolutely nonexistent, according to the genus. The number of joints in the antennæ varies from 12 to 4 in the ☿ and ♀, from 13 to 10 at least in the ♂; that of the maxillary palpi varies from 6 to 1.

Nymphs *always naked*. Larvæ very mobile, without tubercles, but much less independent than those of the *Ponerinæ*. The ☿ disgorge food to them.

5 Formicinæ*. The pedicel has only one joint, the petiole, surmounted by a scale, rarely by a node. The cloacal orifice is circular and provided with cilia. The sting is entirely absent; it is not atrophied, but replaced by an apparatus which acts as a support to the vesicle, which is always pulvinate (see fig. 21 *R*, *E*, *F*, *G*).

These characters are absolute, and they enable us to draw a sharp distinction between this sub-family and the other four.

Antennæ have 12-9 joints in the ☿ and 13 or less in the ♂; the maxillary palpi have a maximum of 6 joints. The nymphs usually spin cocoons, but sometimes remain naked. The larvæ are generally a little more mobile than those of the

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* In 1922 Emery replaced the name CAMPONOTINÆ by that of FORMICINÆ for formal reasons of nomenclature.

Dolichoderinæ. The polymorphism of the ♀ varies; sometimes a ♃ is differentiated.

There is no stridulatory organ. The gizzard is always provided with valves, which are very distinct and strongly chitinous, even when the sepals are absent.

I have described the above characters of the sub-families in detail, in the first place because of their importance, but chiefly because I wish my readers to understand that *even these* are far from being stable; *exceptions* are found everywhere. There is only one sub-family in which we have hitherto found no transitions to the others: that of the *Formicinæ*; its transitions to the *Ponerinæ* must have disappeared during the ages which we now connect with fossils.

There is, indeed, no doubt whatever but that the *Ponerinæ* were the first to appear in the old geological periods. Each of the other four sub-families is directly derived from them. The *Dorylinæ* are their oldest relations. In the genus *Aneuretus*, whose sting is very distinct, the *Dolichoderinæ* have a direct link with the *Ponerinæ*, and the *Myrmicinæ* have a similar link in the genus *Metapone*—whatever Wheeler may say. Finally, the *Formicinæ* possess some remarkable primitive genera : *Myrmoteras*, *Santschiella* and *Dimorphomyrmex*, whose ancestors may well have represented the transition which is still unknown to us.

After this, my problem is to help my reader to make something out of the maze of genera and species which I mention by their Latin names in the manner explained at the beginning of the present chapter, in order to convey some idea of their habits, without inflicting on him fuller descriptions. In order to cut this Gordian knot I adopted a middle course—that of indicating in the first place simply the *number* of sections, tribes and genera of each sub-family, by naming *only* the most important of them and by paying attention to those *facts* which interest us. As the name of the genus invariably precedes that of the species, it would be of no use for me to enumerate the latter here. Thus I will at least supply my readers with the fundamental information they will require for the comprehension of the subject as a whole, and I will avoid all useless padding. In March, 1917, I published a synopsis of the ant fauna of the world. Since then about 7 genera, 16 sub-genera and a large number of species, etc., have been discovered. Nevertheless, I take my synopsis as a basis ; the plates and figures will be an additional help to us.

FIRST SUB-FAMILY, *PONERINÆ* LEPELETIER

5 sections, 11 tribes (5 sub-tribes in the tribes of *Ponerinæ* alone), 64 genera and 44 sub-genera in some of the genera. Note specially the following:

The *Proponerinæ* section, in my opinion, is the most ancient and nearest in many respects to the *Mutillidæ*. It includes for the most part species from India and Madagascar, among others the singular genus *Mystrium* (fig. 3 *A*, and Plate XVI, Part V).

The *Paleoponerinæ* section, two fine examples of which are seen in Plate 1 *a* and *b*, appears to be almost as old as the preceding one. But it has at least one point of resemblance to the *Myrmicinæ* in its extremely constricted postpetiole, which in the genus *Myrmecia* becomes almost a second node of the pedicel.. It can be seen in Plate 1 *a* and *b*.

The tribe of the *Proceratini* is very interesting by reason of its abdomen, whose second segment, following its postpetiole, curves backward and downward in the ☿ and ♀, in such a manner that the following segments, and consequently the sting, are turned forward under the stomach. These very slow moving ants are found in forests under stones or among the moss. I have discovered a new species in Algeria.

In the tribe of *Ponerini* the ants of the sub-tribe of *Centromyrmicini* live in termites' nests, and those of the genus *Harpegnathus* are pictured in Plate XIV *k* (Part V). These are leaping ants.

In the same tribe of *Ponerini* we have the genus *Dinoponera*, which includes one of the largest species in the world, and the genus *Megaloponera*, which during its hunting expeditions produces stridulatory sounds clearly perceptible to the human ear. Another genus of *Ponerini*, the *Diacamma*, and the whole tribe of *Leptogenyini*, have only apterous ergatogynes by way of ♀, and feed almost exclusively on termites. One of these ergatogynes ♀ may be seen in plate III *e*, and compared with its ☿ *d*.

The tribe of *Odontomachini* is remarkable for its mandibles, whose bases are very close to one another and which are provided with two or three long teeth near their extremity only, as fig. 3 *E* shows. These are the leaping ants which we have mentioned elsewhere.

The last section of the *Prodorylinæ* includes among others the genus *Acanthostichus*, in which the ♀ resembles that of the *Dorylinæ*. In all respects, this section forms a transition to the *Dorylinæ*. One of its genera, *Phyracaces*, is pictured in our Plate I *c*. Another genus in this section, *Cylindromyrmex* and its tribe of the same name, bear such a close resemblance to the genus *Metapone* of the *Myrmicinæ* that they may be confused at a first glance. The genus *Sphinctomyrmex* has a notable constriction between every segment of its long abdomen.

Nearly all the *Ponerinæ* belong to the tropical or subtropical fauna of the two continents. A few small species only are found in the North of Europe, Asia and America, or in the temperate regions.

SECOND SUB-FAMILY, *DORYLINÆ* LEACH

2 sections, 3 tribes, 6 genera and 9 sub-genera, all belonging to the genera *Dorylus* and *Eciton*.

The history of the *Dorylinæ* is very instructive. Linnæus and all the old writers mistook their ♂ for wasps or Mutillids, from which they were separated by Leach. Later on, in 1836, Lepeletier came to the conclusion that they were akin to the ants. Shuckard in 1840, though he could not then prove his point, was the first to assign *Dorylus* frankly to the ants, of the genus *Anomma* ☿, while recognizing their affinity with the genus *Thynnus* and the Mutillids. But an error about a find in sugar caused Westwood in 1840 to describe certain ☿ of his new genus *Typhlopone* (a synonym for *Dorylus*) as natives of America, which confused the issue.

In 1890, Savage first discovered some *Dorylus* ♂ going amicably on a plundering expedition undertaken by Anomma ☿. Then at last F. Smith had his doubts and said, rightly enough: "If Linnæus' *Dorylus* are really the ♂ of *Anomma* and not simple parasites, then Jurine's *Labidus* must be the ♂ of Latreille's *Eciton*." He was right. But then a second discovery threw these ideas into disorder. Nothing was generally known as yet concerning the internal anatomy of ants, which I did not work out until 1878, when I separated the *Formicinæ* from the *Dolichoderinæ* as a sub-family. Formerly the postpetiole, then known as the second node of the pedicel, was almost the only means of distinguishing one sub-family from another, among the three sub-families which were distinguished in those days, according to the following dogma or scheme: *Formicinæ*, a single node; *Ponerinæ*, a second node, partially separated from the abdomen by a more or less complete constriction; *Myrmicinæ*, two nodes completely constricted. But in that case how could the ☿ *Eciton*, with their two distinct constricted nodes —creatures which had always been taken, like the *Typhlatta* of India, for modified *Myrmicinæ*—prove to be ☿ *Labidus*, whose pedicels are one-jointed? This upset all our ideas on sub-families, as conceived by Lepeletier.

In 1863, Gerstäcker described the first known ♀ of *Dorylus* and made it into a new genus which he called *Dichthadia*. In 1865 Mayr, in his report on the cruise of the *Novara*, had already made the *Dorylinæ* into a sub-family by including Gerstäcker's *Dichthadia*, as well as the ♂ *Labidus* and the ♂ *Aenictus*, but still putting the ☿ *Eciton* and the ☿ *Typhlatta* into the *Myrmicinæ*. It was not until 1886 that Hetschko, through Mayr, and Wilhelm Müller at St. Catharina in Brazil, through me, definitely destroyed all the old legends by discovering the ☿ and ♂ of *Eciton-Labidus* in the same formicary, which W. Müller even observed in the act of changing its quarters by night. Lastly, in 1890, Gleadow sent me through Wroughton some *Typhlatta*, together with *Aenictus* which had been caught flying from their nest at Thana in India. As early as 1868, Sumichrast had already become possessed of the idea that *Labidus* was the ♂ of *Eciton*, and Jerdon in India had seen ♂ *Dorylus* setting out with some *Typhlopone* ☿, as he wrote to tell F. Smith in 1865. Finally, the discovery by Emery in 1904 of the ♀ of the genus *Leptanilla*, and of the ♂ by Santschi in 1907, confirmed the belief that these ants were minute *Dorylinæ*, according to Emery's correct presentiment.

Since 1877, Emery has contributed a great deal towards the unification of the sub-family of *Dorylinæ*, and the fixing of its characters, especially by means of his remarkable monograph on *Dorylus*, 1895, published in the *Zoologische Jahrbücher*. A summary of the history of the *Dorylinæ* enables us, therefore, to make out the following table of synonyms. It must not be forgotten that the author of the oldest name, defined by characters and recorded in a book or review, is always mentioned before all the other descriptions:

Dorylus F. ♂=*Vespa* and *Mutilla* L. (partially)=*Typhlopone* Westw. ☿=*Dichthadia* Gerst. ♀ (fig. 107 *A*, *B*, *C*, *D*, Part V).

Eciton Latr. ☿=*Labidus* Jurine ♂ (fig. 108).

Ænictus Shuckard ♂=*Typhlatta* F. Smith ☿.

Emery has retained the names *Typhlopone*, *Anomma*, *Rhogmus*, *Dichthadia* and *Alaopone* for African and Indian sub-genera of the genus *Dorylus*, as well as the names *Labidus* and *Acamatus* for sub-genera of *Eciton*. New and interesting genera have been added; *Cheliomyrmex*, the neighbour of *Eciton* of equatorial America, and *Ænictogton* of tropical Africa.

In short, it is a single characteristic of a purely biological nature which distinguishes the *Dorylinæ* sharply from the *Ponerinæ*, especially from their section the *Prodorylinæ:* nomadic life and the absence of permanent nests. All the *Dorylinæ* are rapacious hunters. They find homes, for example, in conquered nests, natural cavities, hollow trunks, etc.; or else they dig carelessly into the shifting soil in order to lay their brood inside, as I observed in 1899 in North Carolina, at the same time myself discovering the first ♀ of the genus *Eciton*. In 1912 the German Consul Schultze did the same for the *Anomma Wilwerthi* and *nigricans* at Entebbe in Uganda, in East Africa. When the *Dorylinæ* have destroyed and eaten all the living animals at their disposal—that is, all those of appropriate size within the widest range they can cover on every side in their hunting expeditions—they move away with their brood during the night, and journey as far as they are able before they establish another provisional headquarters for their depredations. No other sub-family has similar nomadic habits.

THIRD SUB-FAMILY, *MYRMICINÆ* LEPELETIER

4 sections, 22 tribes, 4 sub-tribes, two of which belong to the tribe of *Solenopsidini* (fig. 103, Part IV) and two to that of the *Pheidologetini* (Plate III, fig. *a*, *b*, *c*), 120 genera and 81 sub-genera; this is by far the largest sub-family of ants.

The first section, that of the *Promyrmicinæ*, forms a direct transition to the *Prodorylinæ*, as we have said. It also includes the genera *Sima* (Plate IV *a*) and *Pseudomyrma*, one from the Old World and the other from America, but both tropical, with a preference for living in dry stems.

The large section of the *Eumyrmicinæ* contains the great mass of the genera and species. I may mention the genus *Pogonomyrmex*, whose agricultural habits were described by McCook, our European *Myrmica* (red ants, fig. 5), *Messor*, whose granaries were mentioned by Solomon, King of the Jews, and have been admirably described by the Englishman Moggridge (fig. 110, Part V), the genus *Oxyopomyrmex* (figs. 112 and 113, Part V), with its remarkable eyes, the large genus *Pheidole*, with its distinct soldiers and its ten sub-genera, *Melissotarsus* (fig. 87, Part III) with its curious tarsi, *Cremastogaster* (figs. 99 and 100, Part IV) and its six sub-genera, all able to curl the abdomen up over the back, *Myrmicaria* with its 7-jointed antennæ, *Vollenhovia* (Plate II *b*), *Monomorium* with its twelve sub-genera, one of which (*Holcomyrmex*) is granivorous, *Oligomyrmex*, which includes the smallest ants in the world, and which lives in lestobiosis, the genera *Anergates*, *Epæcus*, *Wheeleriella* (fig. 74, Part III), *Epixenus*, *Hagioxenus*, *Sympheidole*, *Epipheidole*, *Harpagoxenus* (fig. 73 Part III), *Myrmoxenus*, *Formicoxenus* (Plate III *h*, *i*), *Epimyrma*, *Symmyrmica*, *etc.*, which live as parasites upon other ants, the genus *Podomyrma* (Plate II, fig. *a*) the genus *Aphænogaster* (Plate IV *g*), of which Plate II *c* represents an extreme sub-genus, the tribe of *Meranoplini*—large, round ants which roll up into balls—the genus *Leptothorax* with its short hair, the tribe of *Tetramoriini* with the genus *Strongylognathus* (Part IV, fig. 104), which passes from the slave-making to the parasitic stage, the genus, *Triglyphothrix*, in which the hairs are divided into several threads, etc., etc. You see, friend reader, that the *Eumyrmicinæ* section by itself represents a whole ant-world, whose habits promise to be a rich field for study.

The third section, that of the *Rhagomyrmicinæ*, possesses three remarkable tribes. All of them have flattened heads with strong frontal carinæ, situated at the edge of the head and with a pit called the *scrobe* underneath it, which serves to hold the antennæ when they are folded back. The thorax and abdomen are often also more or less depressed, and the legs are often short and prismatic. These are the *Cataulacini*, whose eyes are above the frontal carinæ (fig. 29 *A* and *B*), the *Cryptocerini*, whose ☿ and ♃ have eyes under the frontal carinæ, in the scrobe, as shown in Plate XIV *b*, *c*, and lastly the *Dacetini*, in which the head is flat and triangular, and the eyes are situated at the sides, under or on the frontal carinæ in the ☿ and ♀. The *Dacetini* have other peculiarities of all kinds (fig. 3 *c*), and Plate XVI will offer good examples of these features. The ♂ of the *Rhagomyrmicinæ* have none of the peculiarities of the ♀, ♃ and ☿; they might be supposed to belong to another section.

Lastly, our fourth section, that of the *Mycetomyrmicinæ*, contains the fungus-growing ants, the *Attini* tribe, of which fig. 3 *G* represents a very typical head, with its countless denticulations. In Part V will be found others, with their nests, etc.

FOURTH SUB-FAMILY, *DOLICHODERINÆ* FOREL

2 sections, 4 tribes, 16 genera and 7 sub-genera.

The first section, that of the *Prodolichoderinæ*, contains genera with a more primitive form of gizzard, resembling that of the *Ponerinæ* and the *Myrmicinæ*, which have no special odour and whose anal glands are but slightly developed. Plate VIII shows a type of this section. The sting of the first tribe of *Aneuretini* is still well developed. Fig. 3 *H* shows the head of a curious *Dolichoderus*.

The second section of *Eudolichoderinæ*, with its single tribe, the *Tapinomini*, has a well-developed form of gizzard, shown in transverse section in fig. 12. The sepals of this gizzard are curved back from the base, drawing with them the walls of the crop, which accordingly contain the gizzard wholly or partially. Nearly all the *Eudolichoderinæ* have strong anal glands and emit the well-known volatile *Tapinoma* odour. Plates IV *e*, *f* and Plate VIII *a* show some very interesting types of this section.

FIFTH SUB-FAMILY, *FORMICINÆ* MAYR

3 sections, 10 tribes, 30 genera, 62 sub-genera.

The first section, that of the *Procamponotinæ*, contains only three apparently very primitive genera, each forming a tribe and inhabiting all the Asiatic and African tropics. One of these, *Myrmoteras*, will be shown in Plate VIII *c*. All three have a relatively primitive form of gizzard, with very short sepals.

In the second section, that of the *Mesocamponotinæ*, the gizzard has sepals which are well developed generally, and bent back at an acute angle near the tips, thus forming the continuation of the valves. Among others, it includes a large antarctic and south-tropical genus, the Australian *Melophorus*, with its three sub-genera; one species will be represented in Plate XVI.

The third section, that of the *Eucamponotinæ*, is much the most important and is found all over the world, except among the antarctic fauna, properly so-called.

In the tribe of *Prenolepidini*, the sepals of the gizzard are elegantly recurved but not reflexed.

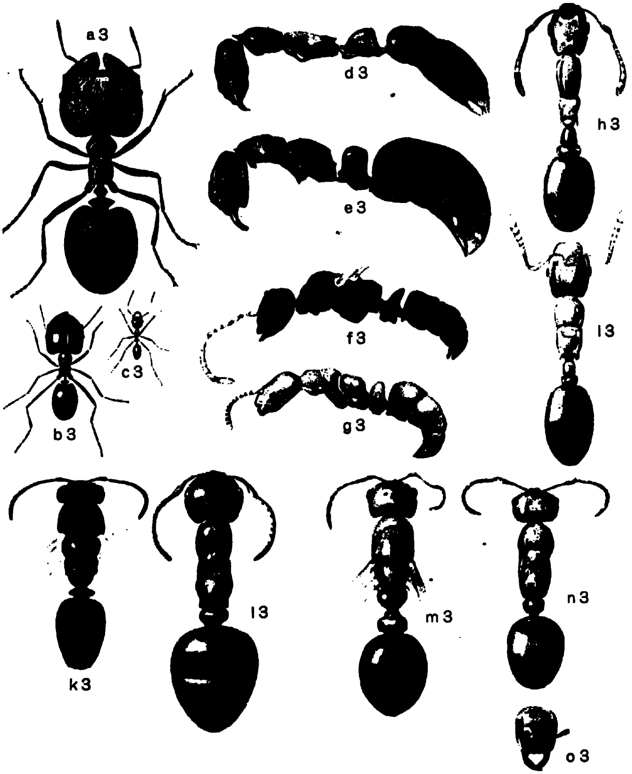
The tribe of *Formicini* includes our *Lasius* of Europe and North America, a singular type of which is represented in fig. 86 (Part III), and also our *Formica* of the same regions, which appear in all their warlike attitudes in Plates X, XI, and XII (Part IV), as well as in figs. 96 and 98. Figs. 75, 78 and 83 (Part III), will show members of the genus *Formica* attending to their toilet, carrying one another about and talking among themselves.

All the polymorphous forms of Huber's famous amazon ant, *Polyergus rufescens*, which belongs to the same tribe, are pictured in Plate III, *k*, *l*, *m*, *n* and *o*. Its bellicose exploits will be represented in figs. 105 and 106 (Part IV). This tribe also contains the sub-genus *Machæromyrma* of the genus *Cataglyphis*, or silver desert-ant, seen in Plate XIV *h* and *i*. Lastly, the American genus *Myrmecocystus*, whose ☿ nurses are drawn on figs. 80, 81 and 82, Part III, also belong to the same tribe, which is perhaps the most interesting of all from the point of view of habits.

The tribe of *Œcophyllini* includes the weaving ants of the genus *Œcophylla*, represented in fig. 131 (Part V).

The fifth and last tribe is immense. In the genus *Opisthopsis*, whose head is shown in fig. 3 *F*, the eyes are situated right at the back. The splendid Australian genus *Calomyrmex* will be shown in Plate IX. Both are specialized. But the great legion is represented by the genus *Camponotus*, with 25 sub-genera, and *Polyrhachis* with 11. Nearly all the *Polyrhachis* are weaving ants, armed with teeth and spines and forming small colonies, preferably under leaves. They

a. *Pheidologeton diversus* Jerd. Large ☿·(♃). 15 mm.
b. Do. do. Medium ☿. 7·5 mm.
c. Do. do. Small ☿. 2·8 mm.
d. *Leptogenys* (*Lobopelta*) *Iheringi* For. ☿. 5·3 mm.
e. Do. do. ♀. 6 mm.
f. *Ponera Eduardi* For., winged ♂. 2·8 mm.
g. Do. do. apterous ♂. 2·6 mm.
h. *Formicoxenus nitidulus* Nyl. ♂. 2·5–3·3 mm.
i. Do. do. ☿. 2·6–3·0 mm.
k. *Polyergus rufescens* Latr. ♂. 6–7·2 mm.
l. Do. do. ergatogyne. 8–8·7 mm.
m. Do. do. ☿. 7·8–9·2 mm.
n. Do. do. ☿. 5–7 mm.
o. Do. do. ☿. Front view of head.



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will be shown in Plates IV *c*, and XIII *b*, *c* and *d* (Part IV), as well as in Plate XV *a*, *b* and *c* (Part V). There the reader will be able to admire their beautiful fleeces, their spines and horns, and their colour. *Polyrhachis* is found almost exclusively in the tropics of the old world, including Australia; one or two are sub-tropical.

But it is the genus *Camponotus*, with its labyrinth of species and races, which surpasses in number all the other ant folk. It will be shown in Plates IV *h*, IX *b* and *c*, XIII *a* (Part IV), and XIV *e*, *f* and *g* (Part V). In addition to this, two *Camponotus* (*Myrmoturba*) *æthiops* ☿, one of which is regurgitating honey-dew to its companion, are displayed on the cover of our book, thus symbolizing the social and moral spirit to which man is always aspiring, though he has never been able hitherto to *attain* to it.

By way of recapitulating, therefore—in 1917, when I made my synoptic survey, we counted among the ants then known to me, 16 sections, 50 tribes, 9 sub-tribes, 236 genera and 203 sub-genera. Since then, about 7 genera and 16 sub-genera have, as mentioned above, been added to these.

If you have succeeded in following me so far, dear reader, you have triumphed over all the difficulties which were an obstacle to your comprehension of the habits of ants and of their social life on our earth. All that remains will interest you without causing you any brain-fag, provided only you have borne the most important things in mind. Phylogeny has made you understand the ancestral origin of ants, ontogeny their individual development and the reason for their polymorphism, external anatomy their structure as seen by the naked eye or through the magnifying glass, internal anatomy the structure of the vital organs of their little bodies; and, finally, classification has made you realize the manner in which we can distinguish their genera, species, races and varieties from one another, taking note, as far as we possibly can, of their phylogenetic descent through the darkness of time.

The two chapters which we have still to cover in the present volume are simple and straightforward.

I would refer all who wish to know of a thorough descriptive account of ants to the magnificent work of Emery, written in the French language: *Genera Insectorum: Hymenoptera, fam. Formicidæ*—a work carried out under the auspices of P. Wytsman, begun in 1911 and not yet entirely finished. (Vertneuil and Desmet, 60-62, rue T. Kint, Brussels.) I have myself described in a brief form, in German (*Die Ameisen der Schweiz*, G. A. Baeschlin, Berne, 1915), all the species, races and varieties of Swiss ants known at the present day. To obtain descriptive details of the ants of the world whose species, etc., have been dealt with in countless journals, a special collection of entomological journals must be made. See also, Bondroit's *Les Fourmis de France et de Belgique*, 1918; though Emery, Donisthorpe and other experienced myrmecologists have, like myself, been obliged to oppose the author's strange attempt to strike out all the races or sub-species with a single stroke of the pen, and to transform the most wretched varieties into species. This summary procedure seems to me inadmissible.

Chapter VI

GEOGRAPHICAL DISTRIBUTION OF ANTS

The genera and species of plants and animals are very unevenly distributed over the surface of the globe. In their distribution, temperature, light and water play the leading rôle. The *flora* of plants and *fauna* of animals is generally poor in cold countries and rich in warm countries; it differs in dry and wet countries and is quite distinct in the sea, rivers and lakes from that of the earth-continents. The seas usually communicate with each other; hence all their flora and fauna interpenetrate one another. But as the continents are to a great extent separated, and differ in their day and night temperature according to season and climate much more than the seas, it follows that the terrestrial faunas and floras differ much more widely among themselves than the marine or even those of the lakes and rivers. Finally, night fauna dwelling underground differ from day fauna living in the air and upon surfaces exposed to the light.

The ants being *terrestrial animals*, we may set aside altogether the seas and their floras—but not water nor plants; for the ant fauna is too largely dependent upon these elements, as we shall see. Nevertheless, how does it happen that various countries with the same, or almost the same temperature, light, seasons, climate and humidity, usually possess entirely a different fauna of ants and terrestrial animals? This reveals the intervention of other elements:

geological history and phylogeny, with which I dealt in Chapter I, and to which I do not wish to return. But let us be clear: I am not speaking of the phylogeny of the polymorphous forms of each sex, but of that of the varieties, races, species, genera, tribes, etc., each taken as a whole. This *specific* phylogeny has causes which are essentially geographical.

A fundamental fact already mentioned is the adaptation of living beings to temperature, humidity, light, etc., by what are known as phenomena of convergence, which confuse the issues of true phylogeny. Black and grey are predominant in cold countries, bright colours in warm climates; under the soil, colours grow pale and eyes disappear; in every desert, psammophores of ants are formed (fig. 11, *A*, *B*) whatever the genus or even the sub-family to which their species belongs. Forms are also frequently adapted by imitative convergence, in what is known as mimicry (imitation of the form, size, colour, etc., of one living being by another). But we must not run from one extreme to the other, and regard everything as the result of convergence. Our real need is to learn by patient and ever-repeated studies the way to *disentangle* true phylogeny, little by little, from the phenomena of convergence.

Geology teaches us that our continents have not always been as they are to-day. For instance, in the far-off past an Antarctic continent connected South America with the present New Zealand. Furthermore, the climates of our earth have changed so much that, in the period known as the Tertiary, countries near the North Pole were inhabited by many animals similar to those of our present temperate climates, so that they had no difficulty in passing from Europe to America and *vice versa* by way of Greenland. In other places, deserts have separated the faunas from one another, and so on.

These different facts have combined to separate the true phylogeny of ants, like that of the other terrestrial animals, more or less completely and at a comparatively early date, into a certain number of major faunas to which geology and history alone can supply the key. On the other hand, we must confess that the indubitable existence of these major faunas has in itself lent powerful aid to geology in reconstructing its history. What, then, are the geographical major faunas, so far as we are concerned?

The reader should be armed with a good atlas of all the countries in the world, and look first at the two hemispheres. In 1910, at the International Congress of Entomology, I gave the following table of major faunas.

	Species and races	Varieties, Geographical and otherwise
1. Neotropical fauna (*a*) South America, with the exception of Patagonia.........	961	208
(*b*) Central America..............	506	121
2. Ethiopian fauna (Africa, South of the Sahara).........	629	125
3. Madagascan fauna (Madagascar, Comoros, Seychelles, Chagos, etc.)...	230	63
4. Indo-Malayan fauna (India, Indo-China, Andamans, Ceylon, Sunda Islands, Philippines and part of China and Japan)..................................	1,165	210
5. Papuan and Oceanic fauna (Moluccas, New Guinea, Oceania)	335	42
6. Australian fauna (Australia, New Caledonia, Tasmania)	380	105
7. Palearctic fauna (*a*) palearctic properly so-called...	152	116
(*b*) Mediterranean (with North Africa, the Sahara, Asia Minor, etc.)	294	158
8. Nearctic fauna (North America).......................	352	105
9. Antarctic fauna (New Zealand, Patagonia)...........	27	3
Total ...	5,031	1,256

We will now analyse these nine world-wide faunas, of which the number of species, races and varieties known has since that date been increased by more than 1500:

1 Neotropical and Central American Fauna

This magnificent fauna arises from the separation of the American tropics from the other continents. It is distinguished by the absence of the genus *Polyrhachis* and nearly all the extremely archaic genera constituting the relicts, that is, the ancient remains of the Old-World fauna, such as the genera *Myrmecia*, *Harpegnathus*, *Mystrium*, *Myopopone*, etc. Nevertheless, it contains one of them, *Stigmatomma*. The sub-family of *Dorylinæ* is represented by the genera *Eciton* and *Cheliomyrmex*, which are exclusively neotropical. But the neotropical fauna also possess special well-developed genera like the *Cryptocerus*, *Procryptocerus*, *Megalomyrmex*, *Pseudomyrma* and *Azteca*. The two last are specialized and adapted to life on trees. They form colonies in the virgin American forests, where they inhabit hollow stems and branches or carton nests (*Azteca*). Enormous numbers of neotropical species inhabit the cavities of plants, living or dead. Some are adapted phylogenetically to these cavities; for instance, certain *Azteca* and *Pseudomyrma* are adapted to the trees *Triplaris*, *Tococa*, *Coussapoa*, *Tachigalia*, *Duroia*, *Cecropia*, etc. The others inhabit indiscriminately the dry, hollow stems of brushwood or other plant cavities; some even (*Pseudomyrma*) the stems of grasses. The gardens formed in the roots of tufts of epiphytes (parasitic plants) by such ants as *Azteca Ulei*, *Camponotus femoratus*, etc., are very interesting.

The principal genera special to the neotropical fauna and its sub-faunas of Central America and Chili are *Typhlomyrmex*, *Cylindromyrmex*, *Belonopelta*, *Paraponera*, *Emeryella*, *Acanthoponera*, *Ectatomma s. str.*, *Dinoponera*, *Neoponera*, *Thaumatomyrmex*, *Alfaria*, *Acanthostichus*, *Eciton*, *Daceton*, *Acanthognathus*, *Megalomyrmex*, *Ochetomyrmex*, *Allomerus*, *Wasmannia*, *Forelomyrmex*, *Tranopelta*, *Forelius*, *Myrmelachista*, *Brachymyrmex*, *Gigantiops*, *Dendromyrmex*, etc. The genus *Pogonomyrmex* is common to this and the nearctic fauna, and the genus *Dorymyrmex* to this and the *antarctic*.

But the most typical group of the neotropical fauna is the *Attini* tribe with its gardens of fungi. The genus *Atta* constitutes its most recent expansion, with the most highly specialized habits. Basing our conclusions upon their habits, which are just as specially adapted as their structure, I think we may assume that they are descended through *Acromyrmex* and *Trachymyrmex* from genera of the little *Attini*, such as the genera *Cyphomyrmex*, *Sericomyrmex* and *Apterostigma*, whose gardening instinct is much more rudimentary as Möller has proved. All the *Attini* are neotropical. I am of the opinion that the whole neotropical tribe of *Attini* is phylogenetically descended from the universal tribe of *Dacetini*, some of whose genera, chiefly neotropical, particularly *Rhopalothrix* and *Basiceros*, closely resemble *Cyphomyrmex*. For the rest, see Chapter I: Phylogeny.

The Chilian fauna is very curious, but still too little known. So far no traces of *Attini*, *Azteca* or *Cryptocerus* have been found. It has distinct affinities with the antarctic fauna, certain of whose forms, such as *Melophorus*, seem to have emigrated to Chili and the Andes, On the other hand, it possesses *Myrmelachista* and a *Pseudomyrma* which are plainly neotropical.

The Central American fauna is only a sub-fauna of the neotropical fauna. It is again sub-divided. Mexico and the Greater Antilles are especially distinct from the rest of the neotropical fauna, whereas a mixture has taken place on the Panama side. The Lesser Antilles are poorer and only in part is their fauna distinctive. The genus *Macromischa* seems to be peculiar to Central America, the Greater Antilles and the Bahamas, the genus *Emeryella* to Haiti.

Moreover, in the neotropical fauna we can distinguish that of the Western Andes, Peru, Bolivia and Ecuador from that of the great basins of the Amazon (Brazil), the Magdalena (Colombia), the Orinoco (Venezuela) and the Rio de La Plata (Argentine and Paraguay). The differences are considerable.

2 ETHIOPIAN FAUNA

This fauna, as a whole, is very homogeneous and much poorer than the preceding one. It is distinguished by the absence of *Ectatommini*, by its relative poverty in *Dolichoderinæ* and its richness in *Dorylinæ* belonging to the tribe of *Dorylini*—that is, the large ants known as visiting ants (*Dorylus*, *Rhogmus*, *Anomma*). The sub-genera *Rhogmus* and *Anomma* are proper to Africa. The genus *Ænictus* is almost the only one common to Africa and to the Indo-Malayan fauna.

It possesses a temperate sub-fauna, that of South Africa, and remarkable desert specializations, chiefly in the Kalahari but also in the Soudan and elsewhere.

The singular genus *Myrmicaria* is common to this and the Indo-Malayan fauna. *Atopomyrmex* belongs to it. The genus *Cremastogaster* is present in a remarkable abundance and degree of complication. In the basin of the Nile, the Ethiopian fauna blends with that of the Mediterranean. Tropical Africa is very rich, especially in large *Ponerinæ*, among which we may cite the genera *Paltothyreus*, *Streblognathus*, *Cacopone*, *Pseudosysphincta*, *Plectroctena*, *Megaloponera*, *Ophthalmopone*, *Hagensia*, *Psalidomyrmex*, *Probolomyrmex*, *Asphinctopone* and *Escherichia*, which are peculiar to this fauna : among the *Myrmicinæ*, the genera *Melissotarsus*. *Diplomorium*, *Dicroaspis*, *Tetramyrma*, *Cratomyrmex* and *Ocymyrmex*; among the *Dolichoderinæ*, the genera *Semonius*, *Engramma*, and *Ecphorella* are special to Africa. The genus *Aphomomyrmex* is almost identical with the American *Myrmelachista*. Finally the relict genus *Santschiella* appears to be peculiar to the Congo.

The differences between the east and west are insignificant in Africa, but quite otherwise in South America—obviously because in the first case there is no chain of high mountains forming a division like the Andes.

3 Madagascan Fauna

This singular and antique fauna of relicts, of which I have made a very special study, extends to the Comoro Islands, the Seychelles, the Amirante Islands, Mauritius and Réunion Island and finally to the Chagos Islands, as I have proved.

It is distinguished by the complete absence of the *Dorylinæ* and *Polyrhachis*. The *Dolichoderinæ* are as scarce here as in Africa. On the other hand the genus *Mystrium*, a relict, of which only one other species is known in Burma, and the genera *Simopone*, *Brunella* and *Eutetramorium* are special to it. There are many special Madagascan *Camponotus*.

Terataner of Madagascar is also related to *Podomyrma* of Australia and New Guinea. The genus *Aeromyrma* of the Madagascan fauna is common to this and to amber and Africa. In fine, it is an antique and special fauna. In its deepest affinities it resembles the Papuan fauna more than any other. Especially on the northern and western coasts it shows signs of old and recent exchanges with the African fauna by mutual immigration of certain African species into Madagascar and of Madagascan species into Africa. The intermediate island Europa has a predominantly Madagascan fauna.

4 Indo-Malayan Fauna

This includes India, Ceylon, Indo-China, South China, South Japan, the Andamans, the Nicobars, the Sunda Islands and the Philippines. It has an important sub-fauna in every island, and also a Ceylonese sub-fauna, another belonging to the Deccan continent, one to Burma and Assam, one to the north-west and finally one to the Himalaya.

In addition to these, the north-west of continental India has a desert sub-fauna (Rajputana) which has important analogies with the eastern Mediterranean fauna—so much so that we may connect them.

The fauna of Assam and that of Indo-China is distinguished from that of the Deccan by its great richness. This magnificent sub-fauna is very distinct from that of the Indian continent proper, and much more akin to that of the Sunda Islands. The mountains of Burma, in particular, retain ancient relicts which are altogether remarkable. *Mystrium Camillæ*, related to *Mystrium Malgache*, is deserving of mention, as well as the singular genus *Myrmoteras*.

Finally the Himalayan fauna is of immense interest. It is the only known mountain fauna, apart from that of the Burmese Alps, which has a considerable number of species, that is, species which are exclusively Himalayan. In a special study which I published, I counted in the Himalayan region 54 ant-forms proper to the district, 51 other forms belonging to the Indo-Malay States, and also found on the Deccan plain and the hills, and finally emigrant palearctic forms especially in the Western Himalayas. The true Himalayan forms for the most part, show traces of their phylogenetic Indo-Malayan or palearctic derivation, varying according to species or varieties.

The fauna of the Andaman and Nicobar Islands has some special forms; but on the whole it has the same features as that of the Deccan and Indo-China.

The Indo-Malayan fauna is extremely rich in *Polyrhachis*, *Ænictus*, *Pheidole* and *Camponotus;* on the other hand, it possesses only three species of *Dorylus* (sub-genera *Alaopone* and *Typhlopone*). Among the relicts we have yet to mention the genera *Harpegnathus* and *Myopopone*.

The Indo-Malayan fauna still possesses the characteristic genera *Odontoponera*, *Cryptopone*, *Trigonogaster* and *Lophomyrmex*, *Rhopalomastix* and the sub-genus *Stictoponera*, not to mention those peculiar to Ceylon. It has the genera *Echinopla* and *Diacamma* in common with the Papuan, Australasian and Madagascan fauna, the genus *Pristomyrmex* in common with the Papuan and Australasian, and lastly the genera *Pseudolasius* and *Liomyrmex* in common with the Papuan. The genera *Dimorphomyrmex* and *Gesomyrmex* are relicts peculiar to Borneo and to amber.

Ceylon has a most curious relict, the genus *Aneuretus* Emery, the only direct intermediate form between the *Ponerinæ* and the *Dolichoderinæ*. *Mesoponera melanaria* of Ceylon has an Australian sub-species. The sub-genus *Hemioptica* Rog. and a few genera such as *Stereomyrmex* and *Acanthomyrmex* are peculiar to Ceylon. The relict genus *Metapone* is peculiar to the Indo-Malay and Australian faunas.

Finally the genus *Rhopalomastic*, of Ceylon and Central India, belongs to the *Myrmicinæ*, and yet at the same time has curious affinities with the *Ponerinæ*, especially in the ♂, and forms the first transitional stage between the two sub-families: actually it is related to the African *Melissotarsus*.

5 PAPUAN AND OCEANIC FAUNA

This rich and beautiful fauna covers the Moluccas, New Guinea, the Bismarck Archipelago and a few other islands.

It has greater affinities with the Australian fauna than the Indo-Malayan. Like the Madagascan fauna, it does not include the *Dorylinæ*, but on the other hand it has many *Polyrhachis*, which are not found in Madagascar. *Podomyrma*, which it shares in common with Australia, is very near of kin to the Madagascan *Terataner.* A host of curious species and genera, *Pheidole* and *Cremastogaster* with ramified spines, etc., lend it a peculiar character : it has the genera *Rhopalothrix*, *Rogeria*, *Prionopelta*, and the sub-genus *Rhizomyrma* in common with the neotropical fauna—which is a very curious and remarkable fact ; we owe it to the researches of Emery, who has made the most important study of this fauna.

It possesses the genera *Podomyrma*, *Epopostruma*, *Orectognathus*, *Rhytidoponera*, etc., in common with the Australian fauna, and the genera *Pheidologeton*, *Vollenhovia*, *Pristomyrmex*, etc., with the Indo-Malayan. Except for one species found in the Celebes, the genus *Trapeziopelta* is confined to this fauna, as well as the genera *Adelomyrmex* and *Wheeleripone.*

The sub-fauna of the Oceanic Islands has been in a great measure invaded and destroyed by cosmopolitan ants and transportations from the continental fauna, as well as from that of the Sandwich Islands. Nevertheless, in various islands (Fiji, Solomon, etc.), there still remain special and remarkable forms, related particularly to the Papuan fauna.

6 AUSTRALIAN FAUNA

This fauna undeniably contains, amongst others, the most beautiful species of ants with metallic colours. It is known as an antique fauna of relicts, with their special further developments. That of the Australian continent may be divided into four principal parts, not to mention the sub-faunas of New-Caledonia and Tasmania. These are:

1 The Australian fauna properly so-called, in the South-East and South.

2 The Queensland fauna, which is extremely rich and forms a direct transition to the Papuan fauna through Cape York and the islands of the Torres Strait.

3 The desert fauna of Central Australia.

4 The fairly distinct fauna of Western Australia.

The Australian fauna is distinguished by the absence of *Dorylinæ*, except for two species of *Ænictus*, so much like some Indian species that I think there is no doubt as to their being of comparatively recent transportation.

The *Dolichoderinæ*, which are extremely abundant, include special genera: *Leptomyrmex*, *Froggattella*, *Turneria* and a great abundance of *Iridomyrmex*. This last genus possesses forms which have been adapted to the plants of the region in somewhat the same way as the American *Azteca*.

Among the numerous antique relicts, we may mention the magnificent genus *Myrmecia* (Plate I *a* and *b*) the genera *Prionogenys*, *Prodiscothyrea*, *Onychomyrmex*, *Dorylozelus*, *Notoncus*, *Opisthopsis*, and the numerous *Sphinctomyrmex*, *Amblyopone*, *Orectognathus*, etc. The genera *Machomyrna*, *Mayriella*, *Dacryon*, *Lordomyrma*, *Myrmicorhynchus* and the sub-genus *Stigmacros* are also peculiar to the *Antarctic* and *Australian* fauna; in the desert fauna of Central Australia, it displays numerous honey-gathering forms, adapted to great droughts (by the provision of honey in the crop). The same obtains with certain *Camponotus* and *Leptomyrmex*.

7 PALEARCTIC FAUNA

The palearctic fauna properly so-called—our own fauna of the woods, meadows and mountains of the temperate and cold regions in the Old World—must be distinguished from the xerothermic fauna as well as from the sub-fauna described as Mediterranean, belonging to the deserts and savannahs. This last is much richer and extends to North Africa, Asia Minor, Central Asia and a part of China, bordering upon the tropical Ethiopian and Indo-Malayan fauna in the deserts or high mountains (Himalayas, Burma).

The palearctic fauna proper, the poorest in the world when considered in relation to its immense territory, is notable for the genera *Formica*, *Polyergus*, *Lasius*, *Myrmica*, *Harpagoxenus* and *Stenamma*, which it possesses in common with the nearctic fauna, for the genera *Anergates* and *Formicoxenus*, which are peculiar to it, for the absence of the *Dorylinæ* and the presence of two species only of *Ponerinæ*, as well as for the absence of *Pheidole*, *Cremastogaster*, *Polyrhachis*, *Monomorium*, *Messor*, *Prenolepis*, etc. It includes but two species of *Dolichoderinæ*, and has the genus *Strongylognathus* in common with the Mediterranean sub-fauna only.

This sub-fauna has only certain *Leptanilla* and *Dorylus*, imported from the Ethiopian fauna, and a species of *Polyrhachis* (*simplex* Mayr) which has come from India as far as Asia Minor. It is characterized by the genus *Cataglyphis* and numerous *Messor* and *Aphænogaster*, but it includes scarcely any *Ponerinæ* but the small species. The Palearctic fauna was destroyed in the Glacial Period, and has not been able to regain its former numbers except in the deserts; this explains its poverty, in particular in those ants which have very few forms specially adapted to cold. The genus *Oxyopomyrmex* (with the sub-genus *Goniomma*), as well as the parasitic genera *Hagioxenus*, *Wheeleriella*, *Epixenus*, *Sifolinia*, *Phacota* and *Myrmoxenus* are peculiar to the so-called Mediterranean fauna. The same obtains with the sub-genera *Proformica* and *Paraformica*.

Iceland and Greenland have no ants, although there are some at the North Cape, for these insects have not found any opportunity of returning thither since the Glacial Period.

8 NEARCTIC FAUNA

Far richer than the palearctic fauna, from which it has only been separated since the comparatively recent Glacial Epoch, the nearctic fauna possesses broadly the same genera, with many more species, some of which only constitute races or varieties of the corresponding palearctic groups. This is the case with *Formica rufa* and *fusca*, with *Camponotus herculeanus* and *fallax*, *Lasius niger* and *umbratus*, *Myrmica rubra*, etc. On the other hand, the nearctic fauna includes parasitic and other special genera—*Epæcus*, *Epipheidole*, *Sympheidole* and *Symmyrmica*. Certain neotropical genera have derivative nearctic forms, such as *Pogonomyrmex*, *Forelius* and *Dorymyrmex*; but more especially *Acromyrmex* (*Trachymyrmex*) *septentrionalis*, *turrifex* and *arizonensis*, as well as *Acromyrmex* (*Mœllerius*) *versicolor* are adapted *Attini* which have migrated from the neotropical fauna. Finally the purely arctic forms come from the old arctic fauna common to the two hemispheres. Chief among these, *Camponotus herculeanus L.* must be mentioned.

A few palearctic species have evidently been recently imported into North America, particularly *Tetramorium cæspitum*.

Finally we must note *Myrmecocystus*, which inhabits the warm dry part of the Western States and extends as far as Mexico, forming part of the Central American fauna.

9 ANTARCTIC FAUNA

This fauna bears no relationship to the arctic fauna, but only convergences due to cold. It possesses one genus (*Huberia*) which is peculiar to New Zealand, and another (*Melophorus*) which is common to these islands, Patagonia, Chili and Australia. The *Dorylinæ* and *Camponotus*, *Polyrhachis*, *Pheidole* and *Cremastogaster* are entirely absent from the antarctic fauna. The tropical genus *Monomorium*, on the other hand, has developed a whole series of forms adapted to cold, which it has not done in the North. Like the antarctic *Melophorus* and *Monomorium*, the sub-genus *Acanthoponera* is common to New Zealand, Patagonia and the South of South America. Two *Amblyopone* here represent ancient relicts (in New Zealand) and two *Dorymyrmex* (in Patagonia and the Argentine Andes) represent the *Dolichoderinæ*. The antarctic fauna also includes, in New Zealand, a *Ponera*, a *Euponera* (*Mesoponera*), a *Discothyrea*, two *Orectognathus* and a *Strumigenys;* that is all, except that Bruch has just discovered a *Discothyrea* in the Argentine!

I will only mention for historical reasons *Camponotus Werthi* Forel, found in the house of the Kerguelen explorers, for this was an imported species from the Cape of Good Hope. No genus that is peculiarly palearctic is found in the antarctic fauna and *vice versa*. The genera *Ponera* and *Strumigenys* are the only tropical genera which are also represented in the arctic and antarctic faunas, though in the second case only in the Mediterranean sub-fauna; these two genera are very widespread—indeed, universal.

10 LOCAL FAUNA

In speaking of the major faunas we have also spoken of their sub-faunas. But over and above these, we find, not only in islands but in small circumscribed countries, special faunas found nowhere else. This is the case with large islands like Formosa, the Philippines, New Zealand, New Caledonia, Haiti, Cuba, even little islands like Coco, west of Panama, the Fiji and Solomon Islands, etc. This is very easily understood in view of their isolation by the sea for thousands of years.

Facts like the following, however, are not so easy to explain:

Travelling in Colombia in 1896, I discovered near the isolated market town of Santa Marta, on the coast of the Caribbean sea, a new and quite special genus which I named *Janetia.* As this name had already been appropriated by another animal, Wheeler inexorably turned it into a synonym and in order to console me, I suppose, named it *Forelomyrmex.* I found numerous and very plainly visible nests belonging to this ant, which was even running about on the roads near Santa Marta, and which I also found at Cienaga, five or six miles away. On the other hand, I was unable to discover any more traces of this species either further to the west, in the country of Barranquilla, or in the east, in Don Diego, Burithaca and Dibulla, or in the south on the Sierra Nevada. After that it was not found again—neither the species not its genus—anywhere in tropical America, except by a single entomologist Gaige, who went to Santa Marta and rediscovered it.

In 1804 Fabricius described under the name of *Formica rapax* a Brazilian *Camponotus* which was not found again for a hundred years. While passing through Copenhagen at the beginning of the XXth century, I saw in the museum the well-preserved original type of Fabricius, and described it afresh. A few years later, Duke sent me from Arriramba on the Rio Trombetas in Para the true *Camponotus rapax*, a native of the same region of the Amazon as Fabricius's type had been, after more than a hundred years. For the sake of greater certainty, I had it verified again at the Copenhagen museum.

In 1915 Mjöberg sent me an enormous *Myrmecia* (☿, 24 to 27 millimetres long, ♀ 30 millimetres) which he had discovered nesting in trees in Australia. This species was absolutely new, despite its size. While in Angola, Africa, in 1886, I gave a description of the little ☿ of one of the largest *Camponotus* in the world, *Camponotus Cæsar.* Since then the same little ☿ has been rediscovered once or twice in the same district. The large ☿ and ♀, as well as the ♂, are still unknown up to the present.

These examples will suffice to show my readers what is meant by terrestrial faunas which are continental and yet *local.* Size is of no importance; it is often the largest species which are local and the smallest which are cosmopolitan. How are we to explain this? As a rule, they are ancient relicts which have doubtless arisen from the remnants of the old, rich fauna of the Tertiary Epoch, and are gradually disappearing. Special circumstances and adaptations to a certain kind of life have been their only means of protection, in some out-of-the-way countries, from complete destruction. Santa Marta, Rio Trombetas and Angola are very far removed from the bustle of humanity. Tree-tops are also safe places of refuge.

On the other hand, other species extend over an enormous area. Our extremely well-known European *Formica* (*Serviformica*) *fusca* is found up to a height of 3,000 metres in the Alps and from the North Cape in Norway to the south of Europe and even China and Eastern Siberia. Its races abound in the United States of America. Our *Tetramorium cæspitum* attains to regions almost equally cold in the north and in the Alps. But these races reach the tropics, not far from the Equator, without going so far in the east.

11 DESERT FAUNA

The sandy deserts bring about curious adaptations in their fauna by convergence. We have spoken of them before and will not discuss them again. Here I wish merely to sum up. The most important points are:

1 The *psammophores*, or hairs which pick up sand (fig. 11 *A*, *B*; also Plate IV *e*).

2 The *nurse* ☿, seen in figs. 80, 81 and 82 (Part III).

During the rains, the ordinary ☿ cram with honey-dew the crop of the nurse ☿, who afterwards serve as sources of food for the community during the dry season.

3 Practically the same explanation applies to the *granaries* of the granivorous ants found in the steppes and deserts. The provisions which they are designed to hold are not *for the winter*, *but for the dry season.*

These three facts, not to mention a few special adaptations, give the desert fauna its peculiar character. Nests in these parts are sometimes very deep.

12 MIGRATIONS

I am not here referring to voluntary migrations like those of the *Dorylinæ*, but involuntary migrations, which are of two kinds: the geological and the historical.

I GEOLOGICAL MIGRATIONS. These can only be proved by inference from certain facts. Thus the many analogies between faunas and floras of the Antarctic has lent support to the hypothesis of an ancient continent now submerged between South America and Oceania. The specialization of the neotropical fauna also tells in its favour; so that the genera common to the neotropical and Oceanic fauna must have been able to emigrate from one continent to another before the submersion in question—their common ancestors, at any rate. Much later, when the Glacial Period had separated the North American ants from those of Europe, the species of the two continents were gradually differentiated from one another; forming dissimilar races, at least, as we said before. There is clear evidence that before this geological period the species were able to emigrate from one continent to another, *except for those which were then already* localized.

On the other hand, something quite different took place in America. Certain species of the neotropical fauna, especially the *Attini* tribe, were formed by an adaptation to the temperate climates of the United States, where I myself, for example, have found one, *Acromyrmex* (*Trachymyrmex*) *septentrionalis*, in North Carolina. This again was a very slow sort of geological migration from one climate to another by transformation of a species or a race. A host of analogous examples could be cited for other faunas. The varieties and races of a species are thus gradually adapted to climates which are colder or drier than that in which their mother-species flourished. I should never come to an end if I were to enter into details; I will therefore stop, especially as there is danger here of becoming lost in the perilous domain of hypotheses.

II HISTORICAL MIGRATIONS. (*a*) *Ancient migrations.* These provide a transition stage to the above. In speaking of the palearctic fauna, we have noticed the absence of ants in Iceland. Now Sparre-Schneider has found nine species of ants in Norway between 68° and 70° North Latitude, east of the North Cape, much farther north than Iceland, whose south coast lies between 63° and 64° north, and also receives the mild influence of the Gulf Stream. But Iceland, as we mentioned before, is seldom visited by ships, and without any doubt no ants have been able to return thither since the Glacial Period. For my part, I am certain that the nine species found by Sparre-Schneider in the north of Norway could live in Iceland if their nests were transported thither.

After the Glacial Period, the climate of Europe became warmer than that of the present day, and as a later result of this, so the geologists tell us, there were warm dry islands called xerothermic islands, which we have already mentioned. Then again there was a slow emigration from the north towards the south, receiving a check in the xerothermic islands, after the migration following the Glacial Period had taken place in the inverse direction, *i.e.*, from south to north. Here we are dealing with geology rather than history. But the following fact is a different matter.

In 1910 I described as a new species a large ant brought from Smyrna in Asia Minor by von Oertzon, and I baptized it *Messor Oertzeni.* It so happened that I myself went to Salonica three months later, and found there numbers of the same *Messor Oertzeni* of a slightly different colour. And what is more, when I went to Smyrna and its neighbourhood by steamboat a fortnight later, once again I found my *Messor Oertzeni*, and this time also in great abundance. Now I could find no trace of this beautiful and very easily perceived ant either in Constantinople, Greece, or Ismid in Anatolia. None of the numerous travellers and entomologists who have been in these regions has found it, either before or since. Another specimen from Salonica was found in a museum. Smyrna and Salonica, as it happens, are separated from one another by the sea, which is continuous from the Bosphorus to the Suez Canal.

But since the time of the Greeks and Romans, Salonica and Smyrna have always been connected intensively and directly by navigation. Hence I felt disposed to draw certain very probable conclusions: (1) that *Messor Oertzeni* was a local species limited to Smyrna and its surroundings; (2) that this ant must once have been imported from Smyrna to Salonica in vessels, in historical, though probably ancient times. We may now consider some other facts which confirm the probability of this hypothesis.

(*b*) *Modern migrations.* The mariner's compass since the days of Christopher Columbus and the steamship for more than a century, thanks to Stephenson, have transformed human navigation. And since then increased navigation has effected more and more transformations in faunas, especially those of the ants, by emigration or immigration. How does this happen? Man's ships have become so many little countries moving on the water. There is everything on board a ship. Crickets sing and cockroaches wander about at night; spiders spin their webs; large cattle and microbes are transported thus, but it is plants and provisions which travel in greatest bulk. Can anyone possibly suppose that my little friends the ants and their fertile females would consent to be excluded from these ships? Far from it; Reh has made a special study of ants brought by ships into the Hamburg docks. He has sent me a very considerable number of species, including some which were previously unknown and which I have described.

But certain ants do more than this; they establish their colonies actually in the ships. One of them, *Monomorium Pharaonis*, must be awarded the palm in this respect. It swarms in every steamer, as soon as the weather becomes warm, when it wakes up and appears in all the wash-stands and wainscots. I have even found a colony of these ants in the handle of a knife which came off the blade while I was dining. Next in order, and scarcely less bold, is *Prenolepis longicornis*. It can be easily understood, then, that ants of this kind brought from the tropics will establish their colonies in our greenhouses, which we warm in winter in order to grow rare plants. Sometimes, even, ants which are themselves rare stray in by mistake. The depôts of colonial produce also frequently serve as shelters for certain ants, even to *Monomorium Pharaonis** at Geneva.

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[1] Quite recently, in December 1924, I received this little ant from the Hôtel Métropole in Geneva, where it lives in the interstices of the woodwork. It is no doubt the central heating which makes life possible for it here and in other Geneva hotels. It would be interesting to know what degree of cold *M. Pharaonis* can stand when the hotel is left empty during a hard winter and the central heating is discontinued for some time.

A certain number of ants which long ago invaded the warm regions of the whole world, by means of ships, are known as *cosmopolitans.* These are the following: 1 *Ponerinæ ; Odontomachus hæmatodes.* 2 *Myrmicinæ ; Monomorium Pharaonis*, *destructor* and *floricola*, *Pheidole megacephala*, *Solenopsis geminata*, *Tetramorium guineense* and *simillimum*, *Cardiocondyla Emeryi.* 3 *Dolichoderinæ ; Tapinoma melanocephalum.* 4 *Camponotinæ ; Prenolepis* (*Nylanderia*) *longicornis* and *vividula.* The cosmopolitanism of ants is not social; it is not an internationalization of their colonies, which remain hostile to one another, but only of certain species which are highly adaptable, prolific, hardy and warlike. These are especially the few species mentioned above, which have invaded certain little islands like St. Helena, the Sandwich Islands, Barbados and others, and have entirely destroyed and supplanted their old, primitive fauna. For instance, in 1899 Perkins sent me from Hawaii twenty species of ants, of which only three were peculiar to the island. Seven were varieties or races of Indian, Madagascan or Polynesian species. Of the ten others, three had been imported from India and Australia, one from the United States of America, and six formed half of the twelve cosmopolitan species enumerated above.

This brings us to a great historic and modern fact: as a result of the struggle for existence inaugurated by navigation, a great many species of ants which were not formerly cosmopolitan are tending more and more to become so. The following examples will illustrate this fact much better than any number of generalities.

In 1852, during a long stay at Madeira, Oswald Heer (*Die Hausameise Madeiras*) very carefully described the habits of *Pheidole megacephala*, which he named *Œcophthora pusilla*, the ant of the Madeira houses. In 1895, Father

Schmitz, who thought he had come in contact with Heer's ant, sent me as such a South American ant *Iridomyrmex humilis* Mayr, which was ravaging houses in Madeira. I wrote to him pointing out his error and requesting him to make a thorough investigation of the surrounding rocks ; and there he discovered *Pheidole megacephala*, which had fled thither for refuge, at the same time confirming my belief that no house ants were left in Madeira except *Iridomymex humilis.* Shortly before this, my colleague Goeldi, then in Southern Brazil, who had sent me from there the same *Iridomyrmex humilis* (humilis means *humble*), replied to my determination by protesting against Mayr's action in applying the word humble to such a daring creature, which was destroying everything in his garden and house, where it lived in the cracks of the walls. Not content with having ousted its brother-cosmopolitan in Madeira (*Pheidole megacephala*), *Iridomyrmex humilis* afterwards proceeded to invade California by crossing the Equator, probably in a ship, and there made ravages which rendered it notorious. Then, in the twentieth century, it passed from Madeira to Portugal, where it nowadays invades houses. It may be predicted that the triumphs of this arrogant parvenu among cosmopolitan ants will continue along so promising a path; it has already been announced in the south of France. But it has emulators in the East.

Plagiolepis longipes, of India, has successively invaded the Indo-Malayan fauna in the east and the Madagascan fauna of Réunion in the west. There it fell in with a rival from South America: *Brachymyrmex Cordemoyi. Triglyphothrix striatidens* emigrated from India in the form of a variety and reached Australia, the Antilles and Mexico, whence other ships bore it to Hamburg, and so forth.

In our warm European conservatories, moreover, the same manœuvres go on. In Zurich, where I once described *Brachymyrmex Heeri*, this ant was afterwards destroyed and replaced by *Pheidole Anastasii* v. *cellarum;* Santschi has now discovered in its place a new *Plagiolepis* which he has done me the honour of naming *Foreli*, and which is of minute size. *Pheidole Anastasii* v. *cellarum* is now invading countless warm conservatories in all countries.

Even our European ants emigrate in ships : *Tetramorium cæspitum* has reached the United States, where I myself have observed its wars, *Lasius niger* Tasmania, and *Formica fusca glebaria*, *Myrmica scabrinodis* and *Lasius niger* Algeria, where I have found them only in the outskirts of a few towns.

To sum up, therefore, it would seem that man's international trade rapidly develops cosmopolitanism in those ants which have the greatest predilection for invasion and which are most generally adaptable, so much so that beautiful and interesting species of local faunae are destined more and more hopelessly to extinction. But are not much the same phenomena occurring under our eyes in connection with all animals and plants? Mice and rats are supplanting elephants, and vermin the rare and beautiful insects. America has given us a phylloxera. In return we have sent the United States our sparrows and white cabbage butterflies, whose progress from year to year Scudder has described by means of graphs, and to Australia we have given our rabbits, which are ravaging the land.

All this is calculated to distress every true lover of nature.

Chapter VII
FOSSIL ANTS

Fig. 29 *A* and *B* represents a fossil ant in Sicilian amber, *Cataulacus* (*Otomyrmex*) *Silvestrii*, described and drawn by Emery.

In 1849, Oswald Heer wrote an account of the tertiary insect fauna of Œningen and Radoboj. In this work he described the first fossil ants known, completing his studies in 1867.

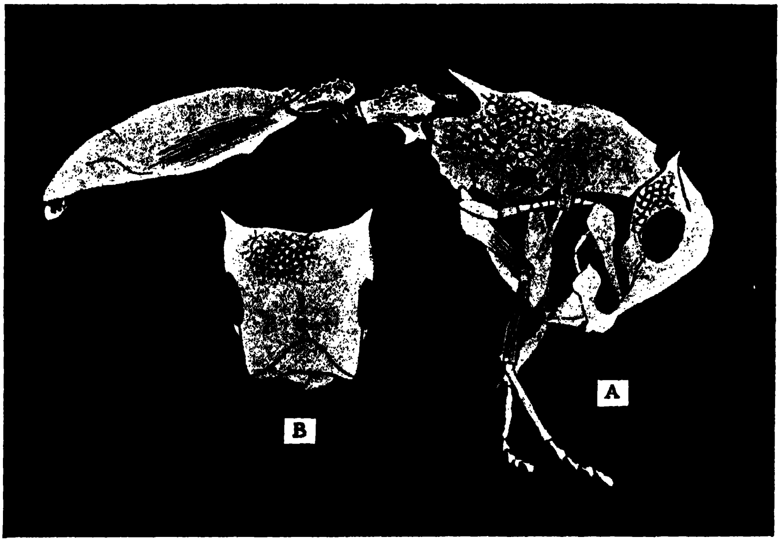

Fig. 29

In 1854, Westwood also wrote on this subject. But the two authors committed several errors which were afterwards corrected by G. Mayr in 1867, by Handlirsch in 1906 and 1908, and by Wheeler in 1910. Wheeler's résumé had the effect of proving that no fossil ant is known which existed before the Tertiary Epoch; the creatures which were supposed to be ants of the Secondary Epoch were nothing of the sort.

While examining the fossil ants in the Scudder collection in the American Museum of Comparative Zoology, Wheeler found that out of some 7,000 ants, scarcely 70 were ☿; all the rest being winged ♂ and ♀. Among these were 139 *Formicinæ*, 25 *Dolichoderinæ*, 85 *Myrmicinæ* and only 27 *Ponerinæ*. F. Smith adds to these a supposed *Anomma* (*Dorylinæ*), but this author cannot be relied upon. As Emery has already observed, these figures are deceptive, for the *Ponerinæ* live on the ground and have few aerial nuptials, so that they rarely fossilized.

Without any doubt, the ants in the Baltic amber studied by Mayr and Wheeler, and next those of the Sicilian amber studied by Emery, constitute by far the finest and richest fauna of fossil ants.* Out of 2,158 specimens examined by Mayr and André, 764 belonged to the *Formicinæ*, 1,130 to the *Dolichoderinæ*, 59 to the *Myrmicinæ* and 25 to the *Ponerinæ*. But nearly all the *Dolichoderinæ* belong to two species only. Wheeler counted among the ants in amber 13 special genera which are now extinct.

In his revision of the whole work in 1914, Wheeler managed to examine 9,527 specimens of ants in the Baltic amber only. The fauna of the Sicilian amber is different,

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* Gust. Mayr, *Die Ameisen des baltischen Bernsteins*, 1868; C. Emery, *Le Formiche dell' Ambra siciliana.*, 1891; W. M. Wheeler, *The ants of the Baltic amber*, Leipzig, 1914.

and belongs to the Miocene Period. Wheeler has made the following interesting comparison: if we took the same genera among the ants of the amber as those already known among our present-day ants, the distribution would be as follows: to the universal genera, 4, to the genera of all the tropics 4, to the tropical genera of our old present-day continents 4, to the present Indo-Malayan and Australian 5, to the present neotropical 1, to our North Temperate fauna (palearctic and nearctic) 6. Total 24.

From the amber discoveries Wheeler has created 6 new genera which are now extinct. This brings their number up to 19.

But on the whole, after examining the matter carefully, Wheeler concludes that the amber fauna corresponds fundamentally to the Asiatic and Australian fauna, to the exclusion of the American and African; the only present neotropical genus found in the amber, *Erebomyrma*, being in all essentials of universal stock.

Among Wheeler's new genera we should mention *Protaneuretus*, which connects the amber fauna with the genus *Aneuretus* and thus strengthens the link between the *Dolichoderinæ* and *Ponerinæ*.

Amber is only fossilized resin dating from the Tertiary Epoch, brought down and washed into the sea. Insects and other animals had been caught in this resin, chiefly while on the wing. They were thus enclosed and admirably preserved until the present-day—much better than all other fossils. These creatures embedded in amber tell us of the magnificent richness of the tertiary fauna, and we can see that in former times the Baltic countries, which are now cold and were then warm, possessed an abundant fauna instead of their present meagre stock.

Moreover, we should do well to note what is taking place to-day in the resins called *copal*, *e.g.*, in the Congo and Mozambique. Copal is found in the earth, and its origin is attributed to the trees of the genus *Trachylobium.* This copal, which is very hard, is full of insects and frequently of ants belonging to our modern fauna, in exactly the same fashion as the Tertiary amber. Magnificent specimens have been sent to me from the Congo, almost undistinguishable from the ants embedded in the Baltic amber except for their colour, which is a paler yellow, even a very light tint. Hence there can be no doubt as to the origin of the Baltic specimens. And yet between one and two million years separate the amber from the copal!

Dear reader, I do not wish to prolong this short chapter on fossil ants. It will prove to you once more that through the feeble understanding we have acquired by comparing the impressions of the outer world with which our various senses have supplied us, transitions in time as well as in space are everywhere to be found. Living objects undoubtedly differ from one another in the qualities they present to us, but an attentive examination reveals so many transitions in these qualities that, even when they appear to be absent, we incur scarcely any risk of error in assuming that the transitional species are altogether extinct, like the vanished genus *Protaneuretus* and its fellows.

And now we will pass on to Part II, which will deal with the sensations of ants, their vital functions, their relations with plants, their guests, parasites and nests.

PART II

Part II

INTRODUCTION

'Vanity of vanities, all is vanity,' cried Solomon, King of the Jews, so they tell us, shortly before his death. He was not thinking then of the ants, though he had held them up as an example to idle humanity, but of man, who in his vanity set himself up on the topmost peak of the Universe and announced that he was created in the image of a personal God of his own invention. In reality, all that man knows and all that he can know about the world which lies around him and from which he issues is revealed to him, not by a God whom he can never know, but through the mediation of the sensations which he owes to his sense organs. These sensations of ours are transmitted to our brains by our nerves; they are elaborated and compared with one another by the aid of our movements, after being conserved by means of the sensory images (engrams) engraved on our brains, and the recall (ecphory) of these images by memory.

In this way, the brain, the organ of our mind, uses that mobile internal concentration of its activity which we call attention, to combine sensations and gradually transform them, in our thought and feelings, into perceptions, representations and abstractions. We use our language, perfected by writing, to give our most highly generalized abstractions the big, fine-sounding names out of which we afterwards build equally big systems, described as *metaphysical*. The vain authors of these systems claim that we ought to *believe* in them absolutely, and that they represent the Absolute of the Universe, whether or not revealed by a man-made God. We need not here concern ourselves further with such matters.

And as for the ants—except for the big metaphysical abstractions which their simple, unwritten antennal language does not enable them to conceive—very much the same things happen to them, in a general way at any rate. Their senses give them information about the external world. They combine these data by means of their movements and their brain. The brain conserves, combines and ecphorizes (recalls) by memory the sense-data, conserving them as engrams in the memory. None the less, there are differences. In their case, the ancestral engrams which have been fixed by heredity and have thus become instinctive and innate are, relatively speaking, infinitely more considerable than they are in our own, and the engrams which are individually acquired and remembered during their shorter lives are infinitely less important. Yet they are certainly present, as we shall prove irrefutably by numerous precise experiments.

Physiology is the study of the functions of the organs of the body. The physiology of animals compared with that of man is known as *comparative physiology*. *Psychology* is the study of the mind, and as our mind is a function of our brain, psychology resolves itself into the physiology of our great brain, as Semon has shown admirably in his study of mnemic sensations, and as the ants, before his time, had already shown me plainly in 1872.

Even our human psychology must needs be comparative, for no man can himself have the consciousness of another. All the same, we *assume* the possession by other men of *self-consciousness.* This supposition is a pure scientific induction. If, therefore, other men besides our *own selves* have a psychology—which we cannot doubt—it is by comparison with ourselves that we assume the fact. Why then should we refuse to grant a psychology to the animals, and, more especially here, to the ants? It may be because we do not understand their language, but then we do not understand even that of *all* men. And language itself very often serves to disguise men's thoughts rather than to express them, as that great *farceur* Talleyrand so aptly remarked.

Pardon this digression, friend reader; it was necessary, to enable you to grasp the fundamentals of the question we are going to discuss right from the beginning of Part II. The first chapter will deal with the *sensations* of ants, compared with our own and with those of other insects, as the basis of their mind and their instincts. In the second chapter I shall speak of the other physiological functions of the ants.

After that, I shall tell you about the special relations of certain ants with plants, and then again, in Chapter IV, about their relations with certain animals which are their guests or which they imitate, or which imitate *them*, or to which maybe they adapt themselves in some fashion or other.

A fifth chapter, closely connected with the fourth, will acquaint you with the parasites, properly so called, which infest formicaries and ants, as well as their monstrosities and poisons, in a word, the *pathology* of ants, that is, their diseases, which may be physical or mental, like our own.

Last of all, a sixth chapter will acquaint you with the dwellings or nests of the ants, and will show you pictures of some of them. There is only a very indirect connection between physiological sensations and the last four chapters, but these chapters had to find a place somewhere, and it was only logical that sensations and physiology should follow after anatomy. Anatomy, I would add, has furnished us with the necessary basis for understanding all the rest, and I hope, therefore, that my readers will bear in mind what they there read, as well as the phylogeny and geography of our little friends.

Chapter I

THE SENSATIONS OF ANTS

A—General Remarks

The starting point of the singular 'mechanism' of instincts is always to be found in the irritation of the sense-organs; if we wish to understand it, therefore, we must get to know these organs and their special functions. We must also study the relations of co-ordination (organization) of the different senses one with another in their action. This brings us to an intimate connection between their functions and those of the nerves, as well as that of the intelligence, which in insects is mainly instinctive. Our task here is to make an experimental comparison between our own mind and that of the insects, without confusing the two, and paying some attention also to the higher animals. We must place ourselves, if I may so express myself, at the level of the insect mind, avoiding, above all, the blunder committed by so many authors—that of attributing to them a human mentality. But we must also avoid going to the opposite extreme, like those who are so fearful of comparing animals with man that they strive at all costs to represent them as 'machines.' A machine which lives, *i.e.*, grows, feeds and maintains its own balance of receipts and expenditure—which, in a word, perpetually carries on its own reconstruction, reproducing by heredity the characters of its ancestors, is no 'machine'; it is something quite different.

In actual fact it is a something to which we have no key, and whose form and functioning are all that we can study, since we have as yet no understanding of its cause and origin. These causes are hidden in a still unknown *sub-cell*, which must be present at the beginning of life in the protoplasm of the egg and its nucleus.

In other words, our task is to avoid two stumbling-blocks: 1 that of identifying the insect mind with our own; and more especially: 2 of imagining that we can construct such a mind in the present state of our knowledge of physical and chemical laws. On the other hand we must recognize that the mind of the ants and the functioning of the senses which brings it into activity are linked, as they are linked in the case of us human beings, by an almost continuous chain of intermediate connections, and that they are derived from the primitive life of cellular protoplasm. This life, specialized in the nervous system by the irritability of the nerves and by its intimate relations with the contractions of the muscles, manifests itself under two aspects, which are like two branches of the same trunk:

(*a*) INSTINCTIVE HEREDITY, inherited by the nuclei of the egg and spermatozoid in conjunction, in the form of hereditary energy or power. It manifests itself in an inevitable and pre-ordained fashion, adapted to the circumstances of a specialized life—that of the variety, the species, the genus, etc. It is this remarkable instinctive adaptation—so intelligent a thing when it goes straight to its predestined end, but so stupid and incapable as soon as we distract it or try to extract anything else from it—which has deceived so many learned men and philosophers by its insidious analogy with the machines we construct, and others, on the contrary, by its analogies with our intelligence.

But, however automatic it may seem to be, instinct is not invariable. In the first place, in its phylogeny it suffers a slow progress of evolution sufficing in itself to explain a certain degree of plasticity, which means the faculty of being modified, in the course of generations. In addition to this, it suffers individual variations which are the more distinct the less profoundly it is fixed by heredity. The divergencies in the instincts of two varieties, for example, will be capable of more individual variability and adaptability than those of the instincts common to all the species of a genus. Finally, if we make a careful study of the manner in which various individuals behave, in a species of insects with highly developed brains, as P. Huber, Lubbock, Wasmann, von Buttel-Reepen, Wheeler, Brun, etc., and myself have done with the social Hymenoptera, we shall speedily discover notable differences among them, especially when we work contrary to instinct. By so doing, we compel the nervous activity of these creatures to display its second aspect, the plastic one, which in their case is largely concealed from us by the enormous development of instinct.

(*b*) PLASTIC ACTIVITY, or activity which is immediately *adaptable* to the environment, is not in any way, as has been claimed, derived from instinct. It is primitive. It is even the fundamental condition of the evolution of life. By adapting itself to its environment, the living being is differentiated. The microbe is plastic. But in order to adapt itself in the same individual to a vast number of different conditions and possibilities, as in the higher mammals and especially in man, a 'brain' needs an enormous number of nervous elements—much more than in the case of the fixed and specialized adaptation of instinct.

From the primitive trunk of protoplasmic life, therefore, is derived in the first place the neuro-muscular system, adapted to the irritability of the senses and muscles by means of the nerves and their central cells (brain, ganglia, etc.).

Furthermore, from this primitive trunk are simultaneously derived two varieties of central nervous activity, or 'neurocyme' (the word neuro-electron would now be used) as I have called it elsewhere.

1 *A plastic activity*, in the true sense of the word, that is, a modifiable activity, by which the individual reacts in an impulsive fashion to every new irritation, and adapts itself as best it can, with less and less success according as it possesses fewer adaptable elements capable of co-ordinating their reaction with the action of the external world. This activity—by reason of its very plasticity—is slower and clumsier, but it has the inestimable advantage of preparing new paths, adapting itself to the unforeseen and so facilitating, through frequent repetition, the automatic activities (habits) which we describe as secondary. The increasing fixation of these activities bears a deceptive resemblance to a gradual passage from plastic activity to instinctive activity. It is true that in a fashion still obscure repeated plastic activity prepares in the germ-protoplasm, by the hidden processes of natural selection and other factors of heredity, the determining factors of hereditary dispositions and complete hereditary automatisms or instincts. Since I am anxious to keep to the realm of fact, I cannot enter here into a discussion on hypotheses concerning the laws of heredity.

2 *An activity described as automatic*, determined and fixed in the individual himself by repetition and a lengthy special adaptation of the plastic activity, which thereupon loses its plasticity. *Secondary automatism* or *habit*, which we observe in ourselves, affords us an easy means of studying how this activity is derived from plastic activity, and how, as it becomes more and more 'mechanical,' prompt, complex and certain (*e.g.*, technical skill), it necessitates less and less

nervous effort. It is much more difficult to understand how inherited instinct, the hereditary automatism, can have derived from the egg, whether fertilized or not, ancestral plastic activities. It seems that a very slow process of selection among the best adapted individuals, and a happy combination of circumstances connecting the life of the species with the surrounding world, may possibly account for it, together with the engraphic radiation in the egg of the characters acquired by every cell of the body. But hereditary energies and the causes of their development or arrest are still so obscure that we had better reserve our judgment on this subject. *Instinct*, said Hering, *is the memory of the species* (Semon's 'mneme'). Moreover, modern physics, with its assumption of infinite smallness in atoms and electrons, finally enables us to conceive the heredity of embryogenesis (genesis of the species through the egg), despite the enormous number of complications it develops in the individual.

In short, every animal has two kinds of activity in various degrees, but it is now one and now another which predominates. In creatures which are altogether inferior, both kinds are rudimentary. In insects, the automatic hereditary activity specialized by instinct reaches its highest stage of development and predominance; on the other hand in man, with his enormously developed brain, plastic activity has risen to unheard of heights, *owing especially to language, and above all to written language, which substitutes graphic fixation for secondary automatism, and allows the knowledge acquired by past generations to accumulate outside the brain*, thus leaving to this brain the strength it requires for the constant adaptation and combination which characterizes plastic activity, without overloading the memory.

You have doubtless learnt, gentle reader, that we have five senses: sight, hearing, smell, taste, and tact or touch, and you have probably heard that it is only certain peculiar people who speak of a *sixth sense*, which we have yet to discover in animals. Well, science has long changed all that. It has decomposed tact into various senses, those of touch properly so called, of heat, of pain, and yet others. It has even proved that the nerves of these three last senses, although intermingled, have different terminations and different bundles of conducting nerves in the spine.

Furthermore, science has shown the existence in us of an eighth sense, the muscular sense or sensomotility. Mach has proved that we feel the acceleration, retardation and rotation of movements independently of sight and touch. Like Breuer, he thought that he could deduce from this a sense of equilibrium residing in a part of our inner ear called the vestibule. But in that case, why is it that deaf mutes, whose vestibule is atrophied, and certain animals which have none at all, do not lose their equilibrium? In any case, *orientation outside the body* in animals has nothing to do with this eighth sense, as I have proved irrefutably in connection with carrier-pigeons, as well as in my experiments with insects.

We must assume that in animals which have no vestibule other sense organs replace it. This is especially plausible for relatively small animals, whose *whole body* is often shaken by the slightest movement of the air, so that in their case the well-known physical law, known as the law of inertia, makes itself felt much less by differences of speed in the displacements of various parts of the body. The slightest disturbances, as well as their direction, are communicated to the whole body and its organs of touch.

Finally, the more capable we are of representing clearly to ourselves all the time, by means of visual memories, the parts of space and the objects it contains, the more incapable we are of representing our muscular innervations, that is, the details of our movements, and their play within the space occupied by our own bodies. It is the same with all the most complex movements we carry out.

To sum up, therefore, all the eight senses of which we are aware in ourselves, and others still which we shall mention later, are to be found in the higher animals and even in insects, with more or less important variations and modifications. This is what we wish to study here in connection with the ants, whose social life supplies us with valuable indications in this respect.

Two senses, smell and taste, are chemical; that is to say they furnish the sensations of living beings with special qualities corresponding to the chemical composition of external objects, either from afar, like *our* smell, by reason of certain emanations from these objects in the air, or by direct contact, like taste. The other senses are physical, which means that they convey to the living being either waves or electrons which determine his sensations from afar, by causing reactions appropriate to the particular structure of the sense organ, as in the case of sight, hearing and heat; or by an immediate disturbance of a part of the nervous terminations of sensory organs which inform him as to the nature of the direct shocks he thus perceives, or as to his own movements, like touch, pain, and the sensation of movement and of equilibrium, or as to needs that he has to satisfy, or again, as to dangers from without. Some of them are special internal sensations, subjective and indeterminable.

B Chemical Senses

a TASTE

The ant's sense of taste, like our own, lies in the tongue, and also in the parts around it, especially on the jaws. I will refer the reader to Part I, Chapter III, and to figures 4 β and γ and 5, which show the organs of taste.

How do we know this? We ourselves have only four distinct sensations of taste: the sweet (sugary), the bitter, the salt and the acid. All the particular savours that we claim to 'taste' are only inspired odours which reach our palate, as can be proved by the fact that a bad cold which obstructs our organ of smell can entirely deprive us of them; professional 'tasters' are well aware of this.

Human taste is only a sense of contact, serving to discern the chemical qualities of non-volatile substances, and to distinguish them from one another by means of a specialized energy, related in quality to that of smell.

Wolff has given a minute description of an organ situated above the pharynx (on the epipharynx) of bees, which I consider to be an organ of taste; but none has been found in the ants.

In 1885, F. Will wrote a monograph on the subject we are discussing. He made a whole series of very careful and ingenious experiments, demonstrating the sense of taste in insects. He used neutral substances by way of control. After he had accustomed some wasps to come to a basket and eat honey, he replaced this honey by alum. The wasps arrived, and deceived by habit, they tasted the alum, but very quickly turned away from it, with bodily contortions. Then he deceived bees and humble-bees by putting honey into flowers and afterwards adding quinine, salt, etc. On each occasion, the insects began by tasting it, but they left the flower as soon as they had perceived the bitter or salt taste. Will found that gustatory perception lasts a fairly long time.

As early as 1874, I had made the following experiments and observations.

When morphine or strychnine are mixed with honey, the ants do not at first perceive it with their antennæ. The smell of the honey attracts them and they begin to eat. But as soon as they have tasted it they draw back. It is easy to observe the preference of the ants for certain foods; they will eat the one for lack of the other, but they will abandon everything, sometimes even their duties and the defence of the nest, for honey, to which they are extremely partial. I have seen ants which were being attacked in their nests and dangerously pressed by others, but which nevertheless stopped for a moment near honey which I held out to them, in order to eat a little.

Ants are not able to distinguish the taste of everything which is harmful to them. Workers of *F. pratensis* gorged themselves with some honey I gave them containing phosphorus. They afterwards remained motionless for several hours, their mandibles separated and their mouths open with an agonized air. Those which had eaten most died; the others gradually recovered.

As a check upon Will's experiments I amputated the two antennæ and the four palpi in several wasps. I then gave them some honey mixed with quinine. Naturally I was obliged to place them in such a position that their mouths touched the honey, as they were no longer able to find it for themselves. They then tasted it, but quickly abandoned it every time. On the other hand, as soon as I gave them pure honey without quinine or morphine, they ate it eagerly. This shows that the gustatory faculty is independent of the antennæ and the palpi, and is located in the mouth.

The gustatory organs of the ants have no hairs; they are simple 'papillæ,' with small orifices moistened by saliva, into which run the fibrils of the ramified nerve.

Needless to say, the few experiments quoted above do not in any way prove that ants, bees, wasps, etc., perceive the taste of their food exactly as we do; and the less so inasmuch as tastes vary even in human individuals. But the analogy is very striking.

b SMELL

In connection with the brain and special sense-organs, we mentioned in Chapter IV of the first Part, which dealt with internal anatomy, the *topochemical smell* of ants. This sense is situated in the last joints of their antennæ, which are often swollen into clubs for this purpose. We may remind our readers of figures 23, 25 and 24 (Part I), in which these organs are represented, as well as their connections with the brain; we shall not deal with them again.

But how are we to prove these organs are those of smell and why do we call them topochemical? Three things are required to justify our opinion: experiment, comparison with ourselves, and reflection. Let us begin with the first.

An ant which has only one antenna left manages without the other, much as a one-eyed man manages with his remaining eye; observation gives more than sufficient proof of this. But as soon as we cut off the two funicles of the antennæ, even if we leave the scapes intact, our ant usually stops short at once, as though stupefied; she becomes incapable of finding her way, of distinguishing a friend from an enemy, of recognizing her cherished larvæ and nymphs, in short, she suddenly finds herself much more isolated from the world around her than a man who is born blind, deaf and dumb, for the man has gradually found out the way to talk and to make his sense of touch serve his purpose.

Nevertheless we must be cautious and draw one distinction: a *winged* ant whose antennæ are cut can find her way while on the wing by means of sight alone, just as well as a humble bee or a honey-bee mutilated in the same fashion; this I have demonstrated especially clearly with the latter. But once she is on the ground, she can neither find her way nor tell what she is about. Hence we must be able to eliminate sight in the case of those ants which see clearly; this can be done by smearing their eyes with opaque varnish which dries rapidly after being dissolved in chloroform. This I have done, as the reader will see. It is much simpler to deal with eyeless ants: for without their antennæ they are entirely lost. All the same, they still think. If honey be applied to their mouths they still recognize it with the mouth and tongue and swallow it eagerly. The contact of another ant causes them to start and separate their mandibles with a frightened air, for they do not know whether it is a companion or an enemy, and behave towards the first as they would towards the second; this I have proved many times. But the manner in which they act varies with the different sub-families, as we shall see later.

In August, 1887, I myself carried out the following experiments at Schliersee (Upper Bavaria) upon *Formica pratensis*, which possesses the best sight of all European ants, and which also has the most poorly developed topochemical smell in its antennæ:

"1 On August 6th, at 8 a.m., I took up my position at the edge of one of the beaten paths belonging to a nest of *Formica pratensis*, seven feet away from the nest, in a place where the regular ant-track crossed a path. I took some ants which were returning from their green-fly with swollen abdomens (crops), a sure sign that their objective was the nest, and I cut off both antennæ from some of them and varnished the eyes and ocelli of others. The ants without their antennæ wandered in all directions, and eventually left the track altogether and remained motionless in a corner. The ants with varnished eyes began by behaving in a similar fashion. Some of them soon died as a result of the manipulations they had undergone from my fingers.

Ants of the sub-genus *Formica*, in the strict sense, are at once very delicate and very irritable, and this renders the operation of varnishing their eyes and ocelli a very delicate one, for they often cauterize themselves by ejaculating their poison whilst they are being held. It was evident, however, that the three which remained in good condition were perturbed. They moved in all directions in the grass at the edge of the path, passing and repassing along the track frequented by their companions, and also missing the way, but retracing their steps without going in the direction of the nest. After a fairly long time, during which I experimented with one of them on a stretch of bare, sloping soil where the ant-track ran (between the path and the nest), it so happened that the first varnished ant, which I had left at the edge of the track, arrived near the slope, following the best road. I then followed her attentively. She meandered a great deal, going first up, then down, much more freely than normal ants. But the nearer she approached to the nest, the straighter she went. At last she moved perfectly well. Whenever she chanced to turn backwards again, it was only for a few steps, and she soon proceeded once more in the direction of the nest. I followed her to the door of the nest, which she entered. The other two varnished ants, more quickly discouraged, crouched under the leaves and would not walk.

2 The following experiments were made on August 8th, on the track of a colony of *F. pratensis*, much larger

than the preceding one, more than forty paces away from the nest, which was situated in a meadow. On the other side of the road, there ran a small scarcely distinguishable path, perpendicular to the road, which was edged with brushwood (with a little turf down between the path and the bushes).

The ants ran over the turf or at the extreme edge of the path. Here I made my first experiments, which dealt in every case with workers returning to their nests, their abdomens swollen with the juices of green-fly.

a First of all, for the sake of comparison, I followed a normal worker for seven paces. She went straight, without hesitating or wandering astray. Once she retraced her steps, but only for an inch or less, and then she turned again in the right direction.

b A worker was carrying a caterpillar to the nest. I cut off both her antennæ with a pair of scissors. She fled from me with a number of leaps and then stood motionless. I gave her back the caterpillar, placing it between her legs, etc. She no longer paid any attention to it, and was no longer able to find the track leading to the nest.

c I cut off both the antennæ of various other workers (generally only the funicles, which, as we have seen, are sufficient), and the result was always the same. They lost all sense of direction, made various circuits, ran across the road frequented by their companions, without noticing it, or maybe running away from any companions they met, and in every case they soon went into corners and remained motionless.

d I varnished *completely* and with care the eyes and ocelli of another worker. I then placed her back on the ant-track, at the edge of the path, quite near the place from which I had taken her, but a little nearer to the nest (about forty paces away). She hesitated awhile, and then took the right direction. But she meandered a great deal, retraced her steps, made sallies to one side, even into the bushes or on to the path. Every time, however, she returned to the right track (frequented at this distance from the nest by a few workers only) and on the whole followed it faithfully, though she sometimes turned back or swerved aside for a distance of 4 or even 8 inches. There was no doubt as to her intention: she wanted to return to her nest; but she had infinitely more trouble in finding her way than the other ants. I watched her follow the right road in this manner over a space as long as seven of my paces, and thus come that distance nearer to her nest. She then reached the road and began at first to cross it well enough. But when she came to the middle she began to swerve from the line followed by her companions, and to fall back down the road. She experimented to and fro in every direction, but became more and more hopelessly lost, wandering adrift and presently going down the road at right angles to the direction that she ought to have followed. A deviation of about a yard from the line she should have followed was enough to make her lose herself. After long and fruitless striving, she went adrift down the road, turned some seven paces away from the right path and was finally lost in the bushes at the edge of the road, under which she effaced herself."

In contrast to taste, which only reacts to direct contact, the sense of smell in the lower animals, as in ourselves, is a sense which reacts at a distance to emanations of a chemical nature. In a word, it is a *special sense enabling the animal to recognize at a distance, by means of some specialized energy, the (chemical) nature of certain bodies.* In order to demonstrate smell, we must first be able to eliminate in an unmistakable fashion our two long-distance physical senses, sight and hearing. But that is not enough. The countless chemical substances contained as vapours in the air and the water (free or absorbed) may, as we know, exercise some sort of corrosive action which irritates nervous terminations other than the olfactory ones—generally (with regard to man at any rate) in a painful or at least disagreeable manner. This is especially the case with the mucous membranes, particularly the conjunctiva of our eye. If a little ammoniac, benzine, chloroform, vinegar, or sulphuric acid be placed near the eye, a painful irritation of the conjunctiva, having no connection with olfaction, can be felt. But whereas we can perceive the odour of the benzine, for example, a fair distance away, we must bring this liquid much nearer to our eye in order that it may affect our conjunctiva. In general, before such irritation can be produced, the irritant substance must be relatively concentrated or very near. Olfaction, on the other hand, is an infinitely finer reaction, which can perceive substances at a great distance, even when diluted almost to infinity (like the odour of musk in the case of man). It is, however, not only by its greater intensity and by fineness of perception, but chiefly by its quality, its 'specific energy,' that olfaction is distinguished from other irritations produced upon certain mucous membranes by gaseous vapours, or liquid solutions.

In our own case, we feel keenly this specific energy which enables us to distinguish a hundred different odours: but how can we prove its presence in others? If we are satisfied with the common plan of placing near an animal certain substances which have an odour for us, and watching to see whether it avoids them or not, we have by no means proved olfaction. We have simply proved that these substances irritated the animal in some way or other. If the animal comes near them instead of avoiding them, we have proof that the irritation is agreeable to it. This does bear a closer resemblance to olfaction, but it is even yet far from proving the fact, for certain irritations of the skin may be agreeable without therefore being olfactory. We must prove, therefore, as I said before, that the irritation in question allows the animal to *recognize* any special kind of matter, to distinguish it from others in a constant and indubitable fashion. We then have the right to speak of olfaction, and this, in my opinion, is the sole proof and sole definition of this sense that we can obtain outside ourselves.

If I prove that a male of *Saturnia* (little night-peacock) which dwells in the woods or at any rate in the country, comes and seeks a female which has been hatched in my room in the middle of a town; that he actually comes and knocks at my closed window and tries to enter my room; if it is not one male but a whole swarm of males of *Saturnia carpini* which thus lays siege to my window, I am right in thinking that I have proved the presence of a special sense in those insects which corresponds to our long-distance olfaction. In 1863, I really did make this observation at Lausanne upon a certain number of *Saturnia carpini*, which I had reared in my room. The swarm of males which came from afar and thronged around my windows after the hatching of my females, which they could neither have seen nor heard, was so great that it attracted a crowd of urchins into the street. The urchins tried to catch these beautiful moths, and marvelled to see them all knocking against my window and entering my room when I opened it. Very similar observations, moreover, had been made by other authors long before my time.

If I prove, over and above all this, that the loss of a certain organ constantly brings about the loss of this faculty of recognition, I have proved this organ to be the special organ of olfaction, such as we have defined it, though the animals deprived of this organ may continue to react to painful chemical irritations, or even to some agreeable ones.

The olfactory lobe and bulb in man are perhaps more rudimentary, comparatively speaking, than those of any other vertebrates except the cetacea; so that we can clearly have but a feeble idea of the world of knowledge and representation which olfactory perception produces in a dog, for instance.

And then there is a fundamental fact to be considered. We are in a bad habit of calling those substances odorous which are odorous for us. Now the study of all animals very soon shows us that differences between animal species are enormous, and that any special substance which is extremely odorous for one species is not so for another, and *vice versa*. The dog, which has an extremely fine sense of smell for certain trails which we are incapable of perceiving, is insensible to odours which affect us in the highest degree, etc. We very soon notice in connection with insects that the faculty of perceiving certain emanations is intimately connected with their way of living, their needs and the dangers they have to avoid. The female of a particular species will have an odour for her male. A particular plant, which attracts an insect from a great distance, leaves the others indifferent and is absolutely inodorous to us. Honey has a strong odour for ants, and roses have none whatever. Here I will quote a few more experiments which I made before 1874, and which are recorded in my *Fourmis de la Suisse*:

"I put into the same phial ants of entirely different species and even genera (*Camponotus ligniperdus*, *Tapinoma erraticum*, and various species of *Lasius* and *Formica*), from all of which I had cut off both antennæ. They intermingled completely with one another, making no distinction; I saw *Lasius* licking *Formica* and *Camponotus*; I even observed the beginning of a regurgitation between a *Lasius fuliginosus* worker and a *C. ligniperdus* worker. These ants did not become aware of the presence of the honey until their mouths happened to get immersed in it; then they began to eat, although clumsily, and in the end they always stuck to it by their front legs, which they were trying to use as probing instruments in the stead of their antennæ. These ants made it clear to me that their intelligence had not suffered in any way, but that they were no longer susceptible to fine sensations. They strove their utmost to take their bearings with their legs, palpi and head, forcing these organs to make unaccustomed movements. When they encountered one another they began mutual probings with their palpi and front legs, and evidently finished, judging by what we have described, by supposing one another to belong to the same formicary. On some occasions, however, I observed certain very emphatic gestures of suspicion, such as a sudden recoil, with threatening movements of the mandibles, but that was not repeated.

Another time, I put some *F. fusca* workers which belonged to the same colony, and all of whose antennæ I had cut off, into a flask with their larvæ, their cocoons and some earth. They did not attempt to hollow out even the smallest chamber for themselves, nor to take the slightest care of their larvæ, which soon perished. They remained like this for two weeks, motionless most of the time, and presenting the most distressing appearance. I had placed among them a worker *F. pressilabris*, also deprived of her antennæ. They did her no harm.

An experiment exactly parallel to this, in which I had cut off the front legs of certain *F. fusca*, above the spur, gave a different result. They soon killed a *F. pressilabris* which I gave them (and also, later on, when I reunited the two groups, the one I had given to their companions without antennæ). They all made attempts to hollow out and build chambers, but in vain. They covered themselves in dirt without achieving anything (they no longer had spurs with which to clean their mouths, etc.). They attempted to take care of their larvæ, but begrimed them all over. Thus in the end they perished, for they had lost the instruments on which (apart from their mandibles) they chiefly relied."

I should like, in particular, to cite verbatim from my original notes a simple experiment which I made on August 17th, 1886, at Fisibach, in the canton of Argovie, following it with the reflections which then occurred to me:

"*Sense of direction.*—I took some *F. pratensis*, with large gasters, travelling from an old nest to a new, and carried them some three yards forward in the right direction. After a moment they all recovered the direction they had been following (from the old to the new nest).

How can that be possible if they only know the road by the mere trail? For how, amongst the hundred-and-one trails of their companions journeying in both directions, could they distinguish the direction of the new nest from that of the old? When they themselves are journeying, they leave their trails fresh behind them, and are thus prevented from returning. But when they are suddenly carried forward, they either perceive some former trail of their own, or else they know the way and direction by the rays of the sun at different times of the day (see below: 'Sight,' in connection with Santschi). For when ants are suddenly put into a place they do not know, even if it be near their nest, they are incapable of finding their way home. This last possibility clearly applies only to young ants or a newly-founded colony."

To these experiments, I will add some complementary investigations also made in 1886, from my *Sensations des insectes.*

"On August 12th, 1886, I repeated the experiment recorded above. I cut off the antennæ of a large number of *Formica sanguinea*, *Formica pratensis*, *Camponotus ligniperdus* and *Lasius niger*, and put them all together in a box. The same facts which I have described above were exactly reproduced. It might have been a caricature of the animals in Oberlaender's paradise, where cats, mice, foxes, lions and chickens licked each other and drank milk out of the same bowl. I saw a *Camponotus* which I had gorged with honey regurgitate some of it to a *F. sanguinea.* A *Lasius niger* strutted between the legs of a *F. pratensis* and a *C. ligniperdus.* Little by little, my various ants huddled piously together, one on top of the other, despite the diversity of species and formicaries. The few rare moments of doubt, the few feeble threats, were scarcely visible, and even those took place almost as frequently between sisters of the same colony as between different formicaries and genera. In the first place (like Hauser), I had tried coating the antennæ with paraffin instead of cutting them off. The effect was the same, but it was less reliable, and the ants were obviously more affected by this than by the amputation. My ants paid no attention of any kind either to the larvæ or the nymphs. They did not even take those which I held for a while under their mouths with a fine pair of tweezers: evidently they did not recognize them.

I then cut off the antennæ of a large number of *Myrmica ruginodis* from the same colony, which I added to the other ants. This time the effect was quite different. The *Myrmica* sharply attacked and bit all the ants they met, *Camponotus* as much as *Formica* and *Lasius;* they curved back their abdomens and stung furiously. Surprised as I was at this unexpected result, I was no less so when I saw, an instant after, that the *Myrmica ruginodis* I had just taken from their nest, where they lived in sweet harmony, were biting, rolling about and stinging one another with an equal degree of fury. I took them all out of the box and reunited them again in another box. There a battle royal began, in which chains of three or four ants bit at each other, etc. This curious result instantly reminded me of the strange experiment made by Belt with *Attini* of the same tribe, which bit each other as soon as a little corrosive sublimate was thrown upon them, and I made this experiment over again and have described it (see Chapter V). Now I was unable to make this experiment succeed except with these particular ants, the genus *Myrmica.* This was such a remarkable coincidence that I think I have found the key to the enigma of the action of the sublimate. As I supposed, it acts upon the antennæ, and, as we now see, it produces upon them temporarily an effect similar to that of amputation. Hence this is evidently a *simple temporary paralysis of part of the olfactory sensibility of the antennæ*, occasioned by the emanations of the corrosive sublimate, even in small quantities. I say 'of part'—for they are still able to find their path again. This fact seems to me to have a real physiological interest.

Moreover, it is plain that the warlike fury of the

Myrmicinæ with their antennæ cut is just as blind, just as incapable of distinguishing a friend from an enemy, as the idyllic calm of the *Formicinæ*. Whence this difference arises we can only conjecture. It is somewhat singular that the loss of smell should produce a peaceful temper in one genus and a warlike temper in the other when they meet living creatures which they can no longer recognize. The experiment is not always equally successful, however, either with the sublimate or with amputation, though I cannot tell why.

My *Myrmica* eventually calmed down after an hour or two, but this was probably owing to the influence of the cold, and it did not happen before there had been several deaths. To anyone who is inclined to attribute this fury in the *Myrmica* to the wound made in the nervous system followed by irritation, my reply would be that this is out of the question, since the amputation of a single antenna produces no sort of analogous effect."

I think, dear reader, that you will now understand the need for experiments—which are cruel, I admit, but no more cruel than what nature is doing everywhere, at every moment—if we wish to get a clear idea of the sensations of insects. I repeated these experiments with bees, wasps, humble-bees, flies, bugs, beetles, butterflies, etc., with varying results, according to the species and the relative development of their sight and of their olfactory peculiarities; what I state, therefore, I have proved.

J. H. Fabre has made the same experiment with night-moths which I have quoted above, and which I made in 1863. But he interpreted it falsely, thinking that it revealed some more or less mystical faculty. Now he himself proved that when he placed the female under a bell-jar and put wax or cement between the edge of the bell-jar and the table on which it rested, the males ceased to fly at this cover; they were no longer sensitive, therefore, to the presence of their females; and thus Fabre worked out his own refutation. He was unable to believe that odoriferous emanations at a distance could have such delicacy and penetrating power as to find their way even under the unclosed base of a cover, and could be suggested by our own very blunt human sense of smell. He did not allow for the *enormous development* of the antennæ in the male.

In connection with taste, we have spoken of the organ on the epipharynx of bees, as described by Wolff, which is also highly developed in wasps. Wolff obstinately maintained that this was the organ of smell, and that the antennæ were the ears of bees and wasps. As it happens I have removed from certain wasps all the front part of the head, including Wolff's organ, leaving the antennæ, and I have proved that they could smell honey at just as great a distance as normal wasps. On the other hand, wasps with their antennæ cut, but with their mouths and heads intact, could smell nothing at a distance and only recognized honey which was placed in direct contact with the mouth.

Again, I have proved that ants have the faculty of perceiving odours at a distance. With the intention of getting rid of the inhabitants of a nest of *Camponotus ligniperdus* hollowed in a tree-trunk, I let these ants starve in my room with the window open, hoping that they would betake themselves elsewhere of their own accord, which they did not do. A fair distance away from them, I had a plaster arena with a high wall, enclosing other ants with some honey. During the night, some ☿ *C. ligniperdus* attacked and knocked down my plaster arena with their heads, all for the sake of gorging themselves with honey which they had never either seen or touched, but had simply perceived by long-distance smell.

All my experiments therefore urged me to recognize that the ant's sense of smell must be *different* from ours. It is unquestionable that the nervous terminations of the sense-organs are arranged and localized in a manner which corresponds to the nature of the special irritations to which these organs are adapted. The retina of our eye perceives a complete image of objects seen by means of light rays reflected upon it by our crystalline lens; we then localize this image in space. Our organ of hearing perceives in succession a 'scale' or series of sounds or tones, following one another; we then localize this series in 'sequences' regulated in time. But the odours we perceive come in a disordered medley to the back of our nose, giving us no clear image of either time or space. Try to represent to yourself a single odour; you will not be likely to succeed, unless at the same time you represent an odoriferous object to yourself by means of sight, sometimes even by means of a musical tone associated with some odour. Herbert Spencer was already aware of these facts when he said that exact relations in space or time are required to bring about engrams clearly associated and susceptible of being rememorized (ecphorized) together, in space or else in immediate series in time. Spencer then spoke of 'relational' senses.

Now the antennæ of insects are an olfactory organ turned outwards, protruding into space, and furthermore, very mobile. This certainly allows us to suppose that their sense of smell is much more relational than ours, that it gives them ideas of space and direction, and that for this very reason it is qualitatively different.

Let us make an assumption—perhaps a very daring one—

that the olfactory bulb and the nasal mucous membrane of vertebrates are the result of the invagination of the antennæ and the antennary ganglia of the invertebrate. The nerve terminations which originally protruded are sunk into a cavity, to which they form a lining, and which is placed in communication with the tracheal organ of respiration, so that a current of air, which is continually being renewed, brings odours to them. I for my part believe that this is what has happened. If so, the antennary ganglion has become the olfactory bulb of man and the higher animals, its nerve terminations are numerous small olfactory nerves, and the cerebral antennary lobe has become the olfactory lobe of our brain.

As we have just seen, their sense of smell enables the ants not only to perceive odours at a distance, as we and the night-moths can, but to feel them in close proximity and even directly, which we are incapable of doing. It is this which I have described as *smell by contact or topochemical smell.* Since the ants are thus able to feel with their antennæ, which are very mobile in all directions, the smells of all the objects in front, to the right and left and even behind when they turn round, as they frequently do, they not only obtain a representation of the chemical qualities they have smelt and felt (see the introduction to Part I, on Hering and Semon), but they can ecphorize them, and recall them at any moment, as well as their forms in space and their sequence in time, which we cannot do with *our smells.* Thus they are able *to recall smells as round, square, elongated, hard, soft, etc., and as having a certain height and being in a certain direction.*

The German scholar, Bethe, claimed that insects had only 'reflex' sensations and movements—photo-reflexes and chemo-reflexes; the Englishman Marshall, on the other hand, attributes to them abstract reasoning powers which are quite human. Both are grossly deceived. Moreover, my friend and colleague, Dr. Rudolf Brun of Zurich, who fully appreciates the value of Semon's work in his *Mneme*, has confirmed my theory of topochemical smell by very careful experiments.

Bethe enticed some ants of the species *Lasius niger*, when on their way to the green-fly, upon two mobile concentric discs over three narrow bands. When he turned the disc from the middle through 360 degrees, that is, the whole way round, the *Lasius* continued their journey as though nothing had happened. But when he turned it 180 degrees, that is half-way round, the ants stopped. From this he deduced that there was 'polarization' of their 'chemo-reflex,' which he considered to be thus neutralized by the reversal of the direction of the scented trails, turned 180 degrees round. Wasmann noticed an error on the part of Bethe in the interpretation of this experiment: the zinc bands retained not only the trails of the *Lasius* which were going to the green-fly, but those of the ones which were returning, so that the tracks were 'polarized' in an opposite direction to one another. Wasmann believed that he could explain the matter in a different way: the ants which were coming from their nest to the aphids were more strongly imbued with their nest-odour than those which were returning from outside. But if this is right, said Brun, how did they distinguish these differences in smells in the midst of so many creatures coming and going in the two directions? Brun thereupon made the following ingenious experiment:

He induced some *Dendrolasius fuliginosus* which were bearing their larvæ to their nest in a dark room to pass over a narrow strip of paper one metre long, leading to some honey placed on a plate. In order to avoid all effects of light polarized in one direction, Brun placed on either side of the large round table, upon which the ants were passing, two equally bright candles, which gave out rays to the ants' eyes in a bipolar fashion, that is, absolutely the same on both sides of them (see below; Santschi, in relation to sight). He then let the ants fall every time from the end of a pencil, in the very middle of the table, upon the strip of paper between the nest and the plate, but always in the wrong direction. The result was usually the same: the *Dendrolasius* followed the false trail regularly for a short distance, and hence moved towards the plate; they then stopped suddenly and sometimes hesitated once more between the two directions, but *they resolutely turned round in the direction of the nest.* We cannot possibly doubt, therefore, that there was something about the trail which guided the ants in their choice of direction and enabled them to correct their initial error. Even certain ants which had never yet passed over the trail in question corrected the initial error in the same way.

But when the larvæ had been carried *for a long time* towards the nest, Bethe's experiment of the 180 degrees neither deceived nor delayed the ants; on the other hand, when Brun suddenly upset the larvæ in the middle of the bridge, they became incapable of finding their bearings, and quite as many of them continued in the wrong direction as in the right.

From all these experiments, and others which would take too long to describe, Brun deduced that probably a *continuous diminution in intensity*, either of the smell of the nest or of the smell of the honey left on the track by their feet (during other experiments), in one direction or the other, may account for the power of the ants to correct their initial error.

We have just seen an example of the disorientation of ants bearing larvæ which were overturned in the middle of a route which they had frequently traversed. But Brun then raised the following objection against himself: '*The ants were made to cross a strip of paper which was uniform in its smoothness and gave them no distinction of forms. What will happen if we change the surface in one direction and make it rough? We shall then see clearly whether Forel is right or not about his topochemical smell.*' So he performed his experiment again, changing the surface of his strip of paper as suggested, and making various rough places on both sides of it. The result was striking. After this, the *Dendrolasius* scarcely ever went wrong. *As many as 75 per cent. of those which had taken a few paces in the wrong direction corrected themselves and retraced their steps resolutely, so as to avoid going wrong again*, even when the experiment was made under the very same circumstances which had completely confused them before on their smooth bridge or strip. Brun thinks this conclusive and now holds that the experiment is sufficient proof of a topochemical smell which makes the ants aware of the forms of objects. Everyone who can read German should refer to pages 186-199 of Dr. Rudolf Brun's excellent little book, *Das Leben der Ameisen* (Leipzig, 1924), where they will find a very good account of these interesting experiments.

Friend reader, this shows you once again how complicated things become when we go deeper into them, and above all, how careful we must be not to suppose that we can explain everything by fine general hypotheses. Future experiments will certainly do much more to *complete* and *rectify* our knowledge of topochemical smell in certain insects, especially ants. Meanwhile, we are obliged to assume as the best interpretation of careful observations and experiments that ants *vary* in their ability to detect smells, according to their genera and species. They perceive at a distance the smells to which their senses are adapted, and in contact they furthermore perceive the forms of odorous objects, *by their smell;* probably they even perceive these forms, in the immediate vicinity of the objects, without contact—although more indistinctly.

We have a somewhat analogous process in the physical sense of temperature at a distance and in contact.

C PHYSICAL SENSES INVOLVING IMMEDIATE SHOCKS TO THE BODY

a TOUCH

As I wish to speak here only of touch properly so-called, I will refer my readers to what I have already said, under '*A* General Remarks,' about its numerous derivations which we shall discuss under *b*, *c*, *D* and *E a*.

The tactile hairs are shown in figures 23 *A* and 25 γ *K*, *R*, (Part I). They are much finer than the club-shaped organs of smell, but, like them, they are movable at the base, which is jointed and possesses a nerve. It is fairly well established by observation that the palpi and their hairs are only organs of touch, which serve to perceive the comparatively strong pressures of objects which they feel, not their smells. Their more or less extensive development does not correspond to that of smell nor that of taste. For the rest, I may refer my readers to what was said in connection with taste about Will's experiments and my own.

It is furthermore evident that neither prostrate pubescent hairs nor ordinary stiff ones, which can be very dense or absent altogether, according to the species, correspond to the keen sense of touch. On the other hand, there are tactile hairs on all parts of the body, but especially on the antennæ. It is very probable, moreover, that certain papillæ, by which I mean certain little raised or sunken portions in which a nerve terminates but which bear no hairs, are also organs of touch.

The following, which has received too little consideration, was published by me as it stands in 1887, and I have already mentioned it in my general remarks:

"The sensibility of insects is characterized by peculiarities other than a sense of touch and analogous to our own. We must remember above all that insects are very small beings, and also, owing to their tracheal circulation (I mean that of the air), very light. On the other hand, the surface of their bodies is generally stiff and hard. *Hence it follows that in their case the result of a touch or a movement of the air is not so much to affect a localized portion of the skin (its tactile hairs) and its nerves, in the way it affects vertebrates or molluscs, as to give the insect as a whole a shock which displaces it.* And by reason of the extreme lightness of most insects, the slightest motion of the air, the most insignificant mechanical shock, a mere nothing—will suffice to produce such an effect and to change the state of the equilibrium. It is true, certainly, that this quivering movement also affects the nerve terminations, especially those of the tarsi, by friction. We must needs conclude that this kind of sensation, and particularly muscular sensation, by which I mean the muscular tensions whose purpose is to re-establish equilibrium, plays an enormous rôle with them. And it is easy to show that this is absolutely true. All entomologists will, as true connoisseurs, bear me out when I say that the slightest air-movement or the most minute shock causes insects to flee at once or makes them fall down from their branches or their leaves, whereas the loudest cries and the sight of a man who is only moving very slowly leaves them for the most part indifferent (I am not speaking here of insects which have strong sight). But over and above this; it can often be noticed that beetles which are on a bush while a fairly strong wind is blowing do not fall off, whereas directly we shake the bush gently they do fall off! This is because the beetles immediately distinguish between these two sorts of shocks. One, the wind, is recognised as harmless, the other reveals the presence of a large living being. On perceiving him, they fold their legs and let themselves fall. These facts may be less striking, but they are none the less true, in the case of ants when climbing on plants. But if anyone wishes to study all the information which this kind of touch can give to a little animal, he should carefully observe the habits of spiders.

b PAIN

Here we have scarcely anything to put forward except hypotheses, which, as my readers already know, I do not like. As we said in our general remarks, for man and the higher animals, the sense of pain is more or less independent of touch. The conjunctiva of our eye has no tactile nerves, and can only feel pain. It is fairly well proved that the terminations of the dolorific (pain-making) nerves of the skin, although they are usually intermingled with those of touch, are different from them. Even in the spine, as Berthelot has proved, the nerve bundles which conduct sensations of pain and heat to the brain are separate from those which conduct the sensations of touch and cold. Nevertheless, there are still unbelievers who think that every pain is only the exaggeration of over-powerful sensations.

It seems to me certain that ants can feel pain, but assuredly infinitely less than we; otherwise no ant could set to work greedily to eat honey a few moments after her abdomen or even her thorax has been cut off. I myself have watched caterpillars, which have been wounded at the posterior extremity of their bodies, turn round and devour their own tails. You will admit, dear reader, that this is going a long way. Caterpillars, however, are not ants.

We have *no idea* as to the possible situation of dolorific nerves in ants as distinct from those of touch. We will therefore choose the wisest course, and say nothing about them.

c SENSO-MOTILITY—EQUILIBRIUM

We feel our movements and maintain our equilibrium unconsciously. How should it be otherwise with those acrobats the ants? I do not wish to repeat what I have already said above in my general remarks about Mach, Breuer and our human 'vestibule,' nor what I have just said while dealing with touch.

Piéron and Cornetz have given the name of 'podometric sense,' which means 'sense that measures walking,' to the faculty which enables the ants to measure the approximate length of the road they are traversing by the sensation of the muscular effort they make while walking. By the aid of their memory ants recall, for example, whether they must swerve to the right or the left at a certain spot during their return journey. Brun proved this in 1916 by means of some experiments with a round table which could be made to revolve from the centre, so as to exclude the scented trail. By ingenious experiments made in an analogous fashion, with the same apparatus, and also excluding all effects of light by means of the bipolar illumination explained above in connection with smell, Brun had already proved in 1914 that ants remember the difference in the efforts they make while climbing up and down

Vol. I.

Pl. IV.[1]

a. *Sima rufonigra* ☿. India. 10 mm.

b. *Rhinopsis ruficornis* (imitating *S. rufonigra*). India. 10 mm.

c. *Polyrhachis* (*Myrmhopla*) *simplex* ☿. India. 6 mm.

d. *Dulichius Wroughtoni* (bug) (imitating *P. simplex*). India. 6·5 mm.

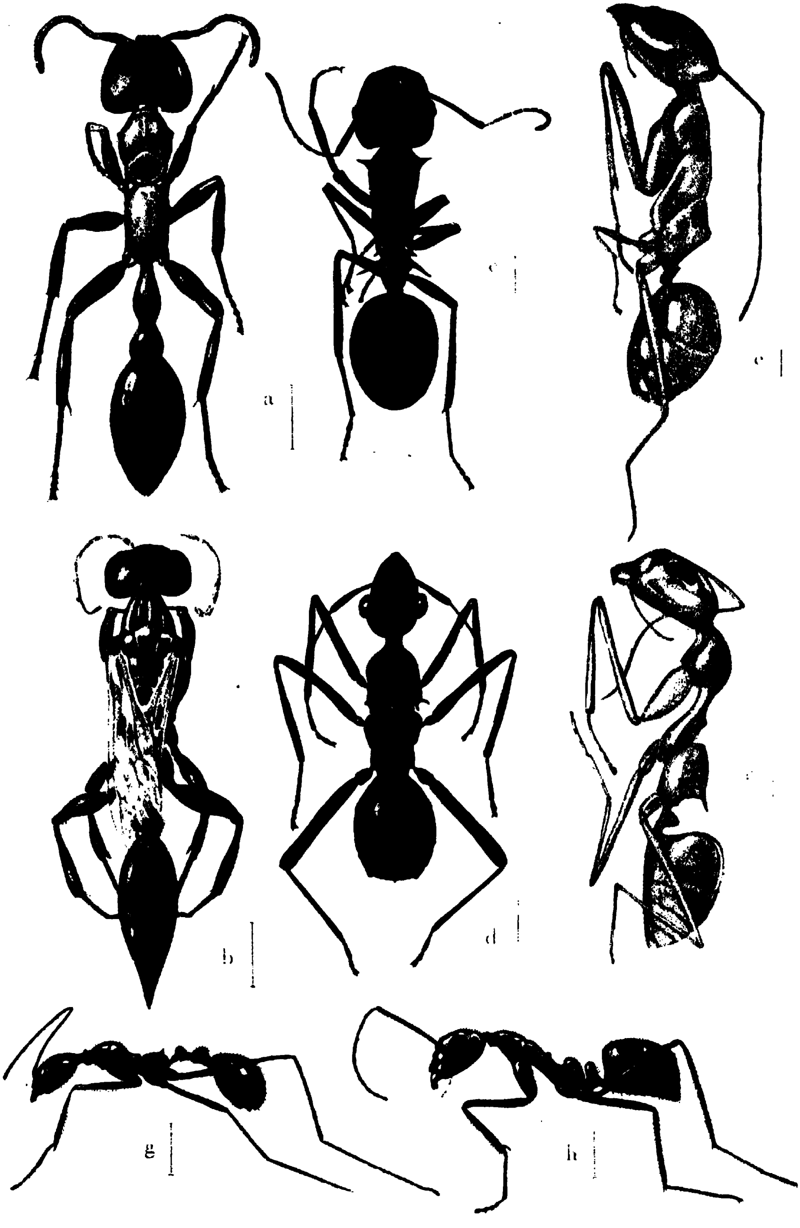
e. *Dorymyrmex* (*Conomyrma*) *exsanguis* ☿. Argentine. 4·2 mm.

f. *Dorymyrmex ensifer* ☿. Argentine. 4·2 mm.

g. *Aphænogaster* (*Deromyrma*) *Swammerdammi* var. curta ☿. Madagascar. 6-8 mm.

h. *Camponotus* (*Myrmosphincta*) *imitator* ☿. Madagascar. 6-7 mm.

Pl. IV.



E. W. Heinrich del. et col.

a slope. He adjusted to his round table, in the middle of which he had placed some honey, the artificial nest of a small colony of *F. rufa*, in such a way that he could raise or lower at will a part of the road which the ants had to traverse when they came out of their nest. He arranged the matter so that the ants had to go uphill on their outward journey. When they came to the honey, Brun quietly changed the slope, placing it in the opposite direction. And on their return journey the ants persistently took the wrong direction—that is, going down—because they remembered that they had had to climb when they first came that way.

And yet ants do not possess the 'vestibule' of the human ear, which preserves our own equilibrium! Whether they have a special organ for the muscular sense or the 'static' sense of equilibrium, we have no notion, and we had better admit our ignorance. We shall deal with the subject again when we discuss hearing and chordotonal organs.

When the ☿ of the amazon ants (*P. rufescens*) are carrying their cocoons, they are no longer able to act in concert or impart direction to one another. All they can do is to follow their own tracks when they come back, without troubling about one another. This was made evident to me as early as 1872 by a remarkable fact. Some amazons had entered an underground nest of *F. fusca*, situated in the turf. Part of the army seemed to have made an attack in an underground passage, whence it came out again laden with cocoons, about two feet further on, though still in the turf. All the ☿ which emerged at this point took several steps in a direction almost exactly parallel to the one that was being followed by the ☿ which came out where they went in. This seems to indicate *a very* *remarkable instinctive memory of the sense of direction, independent of orientation by sight and by the topochemical smell of objects.* Shortly afterwards, indeed, they discovered that they were in an unknown place: whereupon they began to retrace their steps, scattering their ranks and searching everywhere, but without once laying down their cocoons. I watched them for half an hour. Every moment a number chanced upon the right road: they at once recognized it and set out unhesitatingly in the right direction, but none of them went to advise their distressed companions, who continued to search about this way and that until they found for themselves the road which they had taken on their journey out. A few got lost, a long distance away, in an entirely wrong direction. I did not see a single concerted movement, or a single signal which was understood. This forms a singular contrast to the behaviour of an army carrying no burdens, which may lose its way ten times without allowing a single ☿ to be lost.

D OTHER GENERAL OR LOCAL SENSATIONS

The sensations of 'effort,' 'fatigue,' and of a need to relieve oneself may in our own case be localized, properly speaking, in the muscular sense. But hunger, thirst, sexual enjoyment, itching, comfort, discomfort, trouble, etc., are internal sensations forming more or less of a transition to generalized feelings, according as they are relatively more localized, like the first four, or very much generalized, like the last three.

There is no doubt whatever that ants often feel hunger and thirst; trouble is also clearly betrayed in the course of their warfare, and despair sometimes in their defeat. But we judge this only by their actions and by analogy with ourselves; beyond this, we know nothing.

E PHYSICAL SENSES OF PERCEPTION AT A DISTANCE

a TEMPERATURE

As we have seen in our general remarks in connection with pain and heat, these senses act through channels different from those of touch and cold. But heat and cold are distinguished from pain and touch in that man can perceive them both by contact and at a distance. Heat radiations are not the same as light waves, but like them they can be perceived at a distance: thus they form a transition between *C* and *D*.

Ants are extremely sensitive to heat and are constantly on the watch in order to regulate it for their brood, on whose behalf they seek it when the weather is cold and avoid it as soon as the weather becomes too warm. When the temperature drops too far, the movements of all ants become slower and at last they sink down and fall asleep. When the temperature rises, however, they become more and more lively, but their special care then is to avoid drought. We shall see later how the desert ants contrive to preserve a little moisture.

It is indubitable that ants, like ourselves, perceive heat and cold at a distance. Their perception of temperature by contact, on the other hand, is much more difficult to prove for their chitinous skin. But we are entirely ignorant as to whether they possess a special organ intended for the perception of temperature, though it seems unlikely that this is so.

b HEARING

In figure 26 α and β (Part I), we showed the chordotonal organs, and in figure 5 *K*, the stridulatory organs. The latter seem to be lacking in the *Formicinæ* and the *Dolichoderinæ*. As far as I know there is only one ant, *Megalaponera fœtens* of Africa, which stridulates in a fashion that is clearly perceptible to our ears, but many of the *Ponerinæ* and *Myrmicinæ* have stridulatory organs. Nevertheless, this hardly proves that the chordotonal organs are hearing organs, and still less does it prove that they are hearing organs analogous to their own. This was supposed to be so in the first place because they are highly developed in grasshoppers and crickets which certainly perceive stridulation, and in the second place because their structure is analogous to that of the strings of a musical instrument, and appears to answer to the perception of fine vibrations. Lubbock also discovered them in *Lasius flavus*. They are found not only in the tibiæ, but also under the base of the antennæ and in the prothorax.

Apart from crickets, some locusts and grasshoppers, the other insects always appear to remain deaf as soon as we eliminate the mechanical shocks to which all of them are highly sensitive. Lubbock even tried to produce sounds too high to be perceived by the human ear. He succeeded, but no insect reacted to them, and he was obliged in the end to adopt the view shared by Huber, Perris and myself, namely, that hearing cannot be proved in bees, wasps and ants. In spite of this, he persisted in believing that insects hear sounds which we do not hear. I have myself scraped the high strings of a violin an inch or so away from some bees which were foraging in the flowers; I have shouted and whistled with all the force of my lungs equally close to various insects, while protecting them from my breath. So long as they did not see me, they paid no attention. We can hardly give much credence to Léon Dufour, who thought that he had proved hearing in crickets —because they ceased their chirping when he struck the ground with his foot 2 or 3 yards away from them, and in *Annobium* (furniture beetles) because they are silent when a chair is moved. He forgot that the deaf and dumb feel the rumbling of a carriage at a distance.

Sound-waves, especially those of low-pitched sounds, bear a much closer resemblance to powerful mechanical shocks than luminous, caloric or electric waves. Hearing has therefore a fundamental connection with touch, but we human beings make a clear distinction between the perception of a very low sound by touch and the audition of the same sound. We must not forget that man's sense of hearing, having its energy specialized in one organ, has attained to a nicety of detail that has no equal even among the lower vertebrates. This, I consider, is the sense which separates us most widely from the insects and the lower animals. When we come to fishes, the acoustic nerve is confused with other nerves, and the cochlea, that portion of the inner ear which in ourselves is more especially affected in audition, has disappeared.

Miss Fielde produced vibrations on all kinds of instruments—as many as 60,000 vibrations per second—in front of the artificial nests of various species of ants, without obtaining the least reaction. Will, on the other hand, makes incidental mention of an experiment he made upon the beetle *Cerambyx Scopuli.* He enclosed a female in a box, and claimed that every time he irritated her with a pin fixed in the wall of the box and caused her to stridulate, the male which he had placed about 6 inches away would hear her and grow restless and move towards the box. He thinks that insects hear only the stridulations of their own species. By way of contrast to this experiment, I must mention those of Perris, who "made Diptera buzz and scraped the corselets of Longicornes, etc.," some distance away from individuals of the same species, but of different sex, and could elicit no particular response.

All these facts, so it seems to me, combine to show that if insects, particularly ants, have any hearing, it takes place in *some way different from our own*, even in crickets and locusts. We are justified in assuming that they perceive the stridulations of their species as shocks at a certain distance, but in a manner we cannot yet understand very well; nothing more can be said at present.

Wheeler considers that stridulation in the *Myrmicinæ*, *Ponerinæ* and *Dorylinæ* is an important means of communication ignored by many authors. It is, he says, by stridulating that the *Myrmicinæ* attract their companions towards morsels of food. Their swift calls to the defence of the formicary are to be explained in the same manner. The stridulation of *Pogonomyrmex* is perceptible to our ears; when there are numbers of them in a glass flask, other ants perceive the noise through the flask and through their nests, and grow excited. The stridulation of *Atta fervens* is still more powerful, especially in the ♀. Turner found that *Formica* respond to vibrations at the rate of 258 to 4138 per second by rushing outside in an excited fashion. Turner thought that in his experiments he had adequately eliminated the possibility of mechanical concussion from the foundation on which his ants were resting. Wheeler thinks that ants perceive stridulations through the air by their chordotonal organs. Miss Fielde and I remained sceptics in this respect, though we did not deny the results of the experiments made by Wheeler and Turner. I do not deny a certain kind of hearing in ants, but I do not think that their audition is the same as ours; it is, I repeat, quite another thing.

In Part I, Chapter IV, we mentioned the Johnstonian organs and others, as well as the flask and champagne-cork organs of the antennæ, which are there represented in figure 25. For want of knowledge as to the nature of the sense they could possibly serve, they have been attributed to hearing or to some variety of touch, but hitherto without the shadow of a proof.

This is all we know about the ants' sense of hearing. You will admit, dear reader, that it is very scanty, and will be prepared to exclaim, as I did, when I had refuted the long dissertations of so many authors on the seat of insect-hearing: "Heavens! What a large number of ears for such deaf folk!"

c SIGHT—PHOTODERMATIC SENSE

In birds and even in man, sight is the ruling sense; in ants, topochemical smell. At the same time, we should commit a grave error if we were to neglect the rôle which sight actually plays in their case. I have shown clearly by numerous experiments that sight alone *directs*, properly speaking, the flight of aerial insects, including the winged ants. Long-distance smell will draw them in any special direction, but vaguely, without supplying them with precise landmarks; wasps, which have an excellent sense of smell, will afford us clear proof of this difference between the two senses if we cut off the antennæ of some of them and varnish the eyes of others.

I will refer the reader to Part I, more especially to Chapter IV, in which the organs of sight are described. There I have likewise mentioned the theory of mosaic sight, promulgated by Johannes Müller and confirmed by Exner and Grenacher in connection with eyes that have a number of facets, each able to perceive a single ray of light, isolated by black pigment. The facet eyes are specially adapted to distinguish movements. We have proved that these eyes see objects more or less distinctly according to: 1 the number of facets; 2 the degree of convexity and the resulting length of the crystalline lens; 3 the nearness of the object; 4 whether the object or the insect itself is moving more rapidly. But the size of the insect is another factor, as we can see by the following table, in which I have counted the number of facets found in the ♀ and ♂ of two species of ants, and in the small and large ☿ of a third species, indicating also their size:

	Formica pratensis			*Solenopsis fugax*			*Messor barbarus*	
	large worker	female	male	worker	female	male	small worker	large worker
Length of Body	$9^{m}/_{m}$	$10^{m}/_{m}$	$10^{m}/_{m}$	$2^{m}/_{m}$	$6{\cdot}5^{m}/_{m}$	$4{\cdot}2^{m}/_{m}$	$4^{m}/_{m}$	$12^{m}/_{m}$
No. of Facets	600	830	1200	6 to 9	200	400	90	230

A few words must be added for the better understanding of these figures. The small and large workers of *M. barbarus* come out of the nest in the same way and work in the light to an equal extent, whereas the worker of *Solenopsis fugax* nearly always lives underground. The male of *S. fugax*, which sometimes has to seek his female at a great height in the air, has only about 400 facets—less, therefore, than the large worker of *F. pratensis*, which has no wings but a larger body. It would be difficult to understand this proportion were it not that the eye of the male *S. fugax* is hemispherical while that of the worker *F. pratensis* is almost flat; this last mentioned ant, moreover, has one of the kinds of workers which possess the best sight, as they are constantly out of the nest and climb trees.

Nevertheless, there are curious exceptions, like *Cryptocerus Eduarduli* of Paraguay, which I have recently described, and whose ♀, ☿ and ♃ were discovered by Prof. Chodat. The winged ♀ has flat eyes, smaller than those of the worker, which are much more convex. I take it that the ♀ scarcely flies at all in this species. On the other hand, the ☿ *Cryptocerus*, which live on trees, have very good sight. But subsequent biological studies will doubtless explain to us the reason for exceptions like these.

We can observe how worker ants enclosed in glass apparatus, especially those of the genus *Formica*, see through the glass all the movements that are going on and respond by adopting the combative attitude, that is, sitting up on their back legs, curling their abdomens and opening their mandibles. They pay much less attention to motionless objects. I have observed time and time again that the worker ants with the relatively best sight (*F. rufa* and *pratensis*, for instance) continually pass close to the larvæ and cocoons, which are scattered round about, without perceiving them, though they are situated within their field of vision and are being sought for with the utmost patience. A slight movement on the part of the object enables them to see it, or in other words, when they see a movement they become attentive : they afterwards recognize the cocoon with their antennæ. On the other hand, they cannot recognize certain small parasitic flies which often follow them, nor very small ants of other species; they exhibit useless rage and bite at the empty air so long as they cannot feel them with their antennæ.

A large number of small facets diminish the *intensity* of the light perceived by the insect, but increase its faculty of *localization* in space, in other words, the clearness of vision. The convexity of the eye causes it to receive a better impression of light from *various points* in space, and thus of the gradations and intensity of each one, as the insect, the object, or both, move more rapidly. Insects have not our faculty of accommodation, neither have they a pupil like ours, which contracts in strong light. They are dazzled by daylight. A few examples will best enable us to grasp the matter:

One day, for example, I observed a wasp (*Vespa germanica*) chasing flies on the wall of a veranda, as they often do towards the end of summer or in autumn. She darted violently through the air at the flies resting on the wall, In most cases these flies escaped, but she continued her chase with remarkable perseverance, and sometimes succeeded in catching a fly, which she killed, pulled to pieces and carried into her nest, after which she invariably hurried back to continue her chase. At one point on the wall was a fixed black nail, just the size of a fly, and I *very often* saw the wasp mistake this nail and swoop upon it, only to abandon it quickly when she discovered her error by means of touch or smell. Nevertheless, she was led by this same nail to make the same mistake shortly afterwards. I have often made observations like this. We may draw the sure conclusion that the wasp could see objects as large as a fly, but could not distinguish their details; in short, that she saw them indistinctly. A wasp, therefore, does not see movements alone; she also distinguishes the size of objects. When I put dead flies on a table within the reach of another wasp, she came and took them one after the other, and did the same with spiders and other insects of similar size placed beside her. On the other hand, she ignored any considerably larger or considerably smaller insects which I put among the flies. It is very easy to make this last experiment and to trick wasps by setting before them motionless objects the size and colour of flies.

Most entomologists have observed the delicacy and certainty with which the dragon-fly, incomparably the most sharp-sighted of all insects, can distinguish, pursue and catch the smallest insects, while on the wing; their enormous bulging eyes, moreover, are the richest of all, except for the equally well endowed eyes of the butterflies, in the number of their facets. This has been estimated at somewhere between 12,000 and 17,000. Their aerial chase is like that of the swallows. Anyone who tries to catch dragon-flies at the edge of a large pond can easily ascertain for himself how they delight in befooling him, always allowing him to come so near to them that they can only just elude his grasp. In this way it is possible to see how closely they can measure the distance and reach of their enemy. This fact is certain: unless cold or evening overtakes them, dragon-flies always poise themselves for flight at the precise distance which is beyond the reach of the entomologist, and they can see very well whether he is armed with a net or whether he is only using his hands; it might almost be thought, from the way in which we are deceived, that they can measure the length of the handle of the net. They judge their distance so as to be just out of the way of our instrument however far we may lengthen it, and whatever trouble we take to hide it from them by drawing it back and suddenly thrusting it forward. As regards perception at a distance, I will go so far as to say that the light coming from any point reaches more retinulæ (facets) the further this point is from the insect. As J. Müller has already said, this must cause sight to become more diffused as the object moves further off, since the facet is affected by the light of a larger and larger number of different points. *It is probable that this peculiarity enables the insect to measure distance, and to do so more and more clearly as the object comes nearer and nearer (as the angles vary more).*

It is a long time since I was persuaded of the fact that insects with few facets to their eyes see very indistinctly, and I have already said as much in connection with ants. I had suddenly placed a large cluster of *Dendrolasius fuliginosus* (woodland ants, which are accustomed to the shade), in the middle of a lane in the fierce sunlight. I crouched a small distance away. Without any consultation for action, and in spite of the fact that the mid-day sun gave no shade, all the ants began at once to move towards me with their antennæ raised (as though magnetized by me). I moved backwards and they followed me. I then crouched on the other side of their heap; they at once turned round in order to advance upon me afresh. I changed my position again two or three times but they always perceived me. I then moved gently away down the lane; massed in a column, they continued unhesitatingly to follow the straightest line towards me until they were about five yards away, without troubling about one another. Then, however, I veered towards a thicket hard by, till I was actually touching it. As soon as they reached the edge, they ceased following me and entered the thicket. I understood then that the ants had taken me for a tree or something analogous, which they were anxious to reach in order to obtain shelter from the sun. Ants of this genus do not perceive small objects, unless they happen to be in motion and quite near their eyes. It is well known, moreover, that the habits of insects, particularly ants like *Ponera coarctata*, which have only two or three facets to their eyes, bear a close resemblance to those of insects which are totally blind.

Most of the *Eciton* (*Dorylinæ*) have two ocelli instead of composite eyes, but a few species are blind. Thus most of them (*E. hamatum*, *etc.*), go hunting by day in the open air, while ants of the blind species *E. cæcum* Latr., according to Bates, always hunt in covered galleries which they build with incredible swiftness across roads and clearings, until they reach the decayed trunk of a tree or some such object, in whose cavities and rifts they find their prey. I myself have confirmed this fact by experimenting with *E. prædator*, which is nearly blind, in the virgin forest of Colombia.

Lubbock proved in 1875 that bees, like ourselves, distinguish colours very clearly, whereas wasps scarcely do so at all. I confirmed this in 1886, in my *Sensations des insectes*, where I proved plainly that honey-bees and humble-bees readily distinguish colours, especially blue and red, and that it is almost immaterial to them whether the object upon which we place discs of these colours is lighter or darker. But this does not apply to wasps or ants. A German named Hess insisted on contradicting me with his sophisms, claiming that no insect is able to distinguish colours, but he met with no success. On September 1st, 1877, I used some humble-bees which were flying about red, white and blue bindweed, to make the cruel experiment I mentioned in connection with the sense of smell in wasps, and Wolff's organ, which was destroyed with the entire front of the head and the pharynx —*with* or *without* the antennæ. I will describe it here:

Several humble-bees without their antennæ came back to the bindweed, flying from one to another with more precision, if possible, than those which were intact.

In the afternoon of the same day, I operated again upon numerous humble-bees in the trees in the two ways mentioned. None of them came back.

On September 2nd, it rained, but the weather was fine again on the 3rd. I passed by the bindweed again, and found several of the humble-bees, males and little females, whose antennæ I had cut off two days before. They were flying from flower to flower with astonishing swiftness and precision.

I then caught a few male *Bombus pratorum*, which very rarely visited the bindweed and nearly always gathered their booty from the few rare flowers of a foreign blue veronica. From each I cut off *both antennæ, the front of the head and the pharynx in the way described above.* One of them, as soon as he was released, made but a single circuit in the air, came back at once to the flowers and flew straight towards the veronicas. In vain he tried to eat out of them, and went from flower to flower and clump to clump. Then he made equally vain attempts with a few bindweeds, and finally flew away. He behaved exactly like those which had been operated upon on September 1st. Soon there came along a second *B. pratorum*, doubly mutilated, which went straight to the veronicas, exactly as the one before him had done, but not to the bindweeds. I caught hold of him and verified the absence of the two antennæ and the front of the head.

I mutilated in the same way several *Polistes gallicus* (a kind of wasp) which were visiting the mignonette. They behaved in exactly the same way as the humble-bees had done. Some of them came back and flew at once to the mignonette, where they tried in vain to eat.

During these experiments, I usually noticed that the loss of the antennæ, far from rendering the insects uncertain in their flight, seems to *increase* their precision. They no longer balance themselves first to right and then to left in the air before settling, as wasps in particular usually do, but they fly in a straight line towards a point and settle immediately, like flies and dragon-flies.

The balancing movements in flight are caused, therefore, by a function of smell. But we must return to our ants, which, so far as I can judge, do not distinguish the colours that a normal man distinguishes: they appear to be complete Daltonists—which means to say that they only distinguish between various degrees of light; between a pale shade and a dark.

On the other hand in 1886, acting upon the competent advice of Soret, Professor of Physics at Geneva, I checked and perfected Lubbock's experiments. This author had proved that ants have an intense perception of the luminous rays we call ultra-violet, which normal man scarcely ever perceives, but which have a strong physical and chemical action. Since that time Vitus Graber and other authors have proved that the lower animals which have no eyes can nevertheless perceive light through their skins. Some of them (the photophobes) avoid it, while others (photophiles) are attracted by it; but this is not *sight* and has nothing to do with the optic nerve, nor even with a localized primitive eye. It is evidently a sensation analogous to our own of heat and cold. It is very probable that this sensation of light through the skin is much more highly developed in blind ants than in ants which can see, but I have not been able to experiment on them because we have none in Switzerland. However that may be, in my complicated experiments of 1886, of which I can give but a short résumé here, I was obliged to eliminate heat and to allow for the sense we describe as *photodermatic*, which perceives light by the skin without the aid of eyes.

Soret drew my attention to the fact that our human crystalline lens has a great power of arresting and absorbing the ultra-violet rays; this is the chief reason why we do not see them, whereas those who have been operated upon for cataract see them as lavender-grey. In order to intercept completely, in other words to suppress, the passage of the ultra-violet rays, I followed the advice of Soret and used a cell 1 centimetre thick, full of a concentrated solution of *esculine.* Furthermore, in order to absorb as many as possible of the other rays of the spectrum while allowing as many ultra-violet rays as possible to pass, I used a glass of dark cobalt. To eliminate as far as possible the radiant heat, I used a layer of water between 6 and 8 centimetres thick, which according to Soret, sensibly arrests half of the total heat of solar radiation. A glass of a fairly dark red shade served me for the control experiments. It is a specially good conductor of heat rays, but apart from that produces an effect upon ants analogous to that of esculine. Finally, to obtain complete darkness, I used a piece of pasteboard 3 millimetres thick.

I first chose a large species, *Camponotus ligniperdus* Latr., which in addition to its height has the advantage of possessing no frontal ocelli. I then tried to cover the eyes of these creatures completely with varnish. As they at once proceeded to rub off the varnish with the comb of the spur on their front legs, I chose an old opaque white varnish which had been thoroughly dried. When I dissolved this varnish in a little chloroform and put it immediately on the ant's eyes with a cataract needle, holding the legs meanwhile, it dried up very quickly and adhered firmly. The coating of varnish is never thick enough to intercept entirely a light which is fairly strong, even if diffused. In my last experiments with *Formica sanguinea*, a few workers and a female of *Formica fusca* L., I tried to guard against this difficulty by adding to my varnish a strong dose of perfectly dry tar, so as to make it nearly black. I thus obtained a considerable but not absolute opacity. In this way I made more than 45 very varied experiments by day and night with different ants, spending several hours and sometimes even several days upon each. They are to be found described in my work on the sensations of insects.

Their result can, I think, be summed up in a few words: 1 *Ants perceive light, and more especially ultra-violet rays, as Lubbock proved.* 2 *They seem to perceive ultra-violet rays chiefly with their eyes, in other words, they see them; for when their eyes are varnished they show that they are almost indifferent to them: under those circumstances they give no noteworthy reaction except to direct or at any rate strong sunlight.* 3 *The above experiments seem to indicate that photodermatic sensations are weaker in ants than in the lower animals studied by Graber.*

I afterwards made a few experiments upon a man who was totally blind, to find out whether he had any sensations comparable to the photodermatic sensations, but as soon as I had entirely eliminated hearing, temperature and all movements of the air, he was incapable of distinguishing light from darkness. This, we must hasten to observe, does not in any way signify that his lower nervous centres, ganglia, spine, etc., have no sensations of the kind, but only that his superconscious 'self' knew nothing of them.

After writing the above, I received *Eyeless Sight* by Jules Romains,* the results of whose experiments are contrary to all our present ideas. According to him, man possesses in the little 'menisci' described by Ranvier, in other words in his epidermis, a number of *ocelli*, which are capable in the aggregate of perceiving daylight. If well-chosen subjects are hypnotized and patiently educated in their unconscious state, they succeed in seeing objects

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**La vision extra-rétinienne et le sens paroptique* (Paris, 1920) by Louis Farigoule (Jules Romains). [The English translation—by the translator of the present work—appeared, with additional material, in 1924.]

and even reading with their eyes bandaged. Jules Romains claims that the experiment succeeded in the case of men blinded in the war. These statements need confirmation. So far as ants are concerned, I refer the reader to our remarks on the *Anomma*, in Part V, Chapter 1.

In 1902, with the personal collaboration of Henri Dufour, Professor of Physics at Lausanne, I made some very exact experiments in his laboratory, absolutely excluding all rays of the solar spectrum except the ultra-violet. These experiments, made upon *Formica sanguinea* and *fusca* with cocoons, entirely confirmed those of 1886. I then took advantage of the occasion, however, to submit the same ants to the action of the Röntgen or X-rays, which were then just coming into prominence. The result this time was entirely negative. The ants did not react in any way, and a week after the experiment they were as well as they had been before. Dufour himself confirmed the positive reaction of ants to ultra-violet rays and their negative reaction to X-rays. It may be added that ants react more strongly to ultra-violet than to blue, green, yellow, or even violet; they give scarcely any reaction to red.

Summing up, therefore, it has been proved that ants see more or less distinctly according to the development of their facet eyes and according to their species, as well as their sex. They distinguish movements especially well, but objects very poorly when they themselves are moving: they do not appear to discern colours as such. Their sight, unlike their sense of smell, is always inferior to ours: but both are different in quality from ours. The peculiarities of their reactions and their habits are thus explained to a considerable extent by those of their sensations, which we unreflecting human beings assume to be the same as our own.

As for the three ocelli of the vertex, their function is still very ill-understood. I have taken it for granted that they are used for seeing near at hand and also in the semi-darkness of the nest. This obtains especially with winged ants, which need this double adaptation; it would be useless to butterflies and dragon-flies, for instance. Von Buttel and others subscribe to my way of thinking, but it is a mere hypothesis, with which I am only half satisfied.

Finally the following ingenious experiment was made by Santschi in Tunis. Using a large screen, he threw a shadow over some ants which were returning to their nest in the sand, and then by means of a mirror he projected the sun's image in the opposite direction. Soon the ants, deceived by this false sun, also turned round and moved straight away from their nest. When he repeated this experiment at a somewhat different angle, Santschi saw them continue to follow the false sun of the mirror. This experiment succeeded even with files of ants which were following their ordinary path.

Brun confirmed this with our European *Lasius niger*, as will be seen in fig. 85 of Part III. An ant walking on sand set out towards her nest, almost straight towards the sun. Brun stopped her suddenly at a point X, and placed over her an open box, inverted. It was then 3 o'clock in the afternoon. At 5 o'clock Brun lifted the box and set the *L. niger* free. She set forth again, but this time at an angle of 30 degrees to the right of her former direction, which was exactly as far to the left as the sun had turned during the two preceding hours. In the case of another ant similarly imprisoned for an hour and a half, the variation was only 25½ degrees, and in a third, imprisoned for two hours and a half, 37 degrees.

But Brun hastened to add, rightly enough, that these experiments did not always succeed, for memory, combined with topochemical smell, often enables the ants to correct their error at once. It is the same with other visual perceptions, like that which guided the column of *Lasius fuliginosus* towards my body, as quoted above. When their perceptions are purely visual, ants generally keep their antennæ in the air and do not feel the ground with them.

To sum up, therefore, ants orient themselves by combining their sight, when they have such a thing, with topochemical smell, touch, senso-motility and their sense of heat—and sometimes, possibly, with the vestiges of a problematic sense of hearing.

Chapter II

PHYSIOLOGY AND PSYCHOLOGY OF ANTS

Physiology is the study of the functions of our organs, and *psychology* the study of the mind: if you have followed me clearly thus far, dear reader, this chapter may well be short, for in speaking of the anatomy of our little friends' organs, I have pointed out their functions, and the ant-sensations which we have just been studying provide us with the key to their little minds—which seem small in our eyes, it is true, but which are a very long way ahead of our own in social matters, as we have seen.

In the internal anatomy we described five different pump-systems, including three which are individual—one consisting of respiration by the tracheæ, another of a heart without veins or arteries, suffused in white blood, and one of the gizzard-bulb, which empties its contents into the ant's digestive system. But the two other pumps, which are exclusively social, are much more interesting.

STARVATION. When she caused the young larvæ of *Aphænogaster fulva* to be insufficiently fed by small ☿, which were themselves inadequately nourished, Miss Fielde always obtained dwarf ☿ from their nymphs, similar to those brought up by the fertilized ♀ soon after the foundation of the colony. This fact is very interesting, but it affords no explanation of polymorphism, as we have seen in Chapter II of Part I.

Miss Fielde starved various ants, giving them nothing to drink except distilled water on a disinfected sponge. The results were as follows:

1 Thirty *Cremastogaster lineolata* ☿ lived for eighteen or nineteen days.

2 Thirteen *Camponotus pictus* ☿ lived seven to twenty-nine days; three of them were killed and eaten by their companions. This was the only case of the kind observed by Miss Fielde.

3 Nine *Aphænogaster fulva* lived eighteen to forty-six days.

4 Eight ☿ *Camponotus pennsylvanicus* lived fourteen to forty-seven days. One of them made fruitless endeavours to regurgitate honey-dew to a companion on her thirty-first day of fasting, and the other did the same on her thirty-sixth.

5 One of two *Camponotus castaneus* lived for fifty-four days, the other more than a hundred days.

6 Nine ☿ *Formica subsericea* lived seventy-one to a hundred and six days.

The longevity of these two ants surpassed that of the most famous human starvation-cases. Miss Fielde adds that the starving ants remained active and died in the end quite suddenly.

7 A winged ♀ *Camponotus castaneus* regurgitated honey-dew to her fertilized sister on the twenty-first, thirty-fifth, fortieth and sixty-second days of fasting, and in such a way that Miss Fielde was able to watch for several minutes the transfer of the regurgitated drop.

Starvation is an excellent way of forcing an ant to beg for regurgitation, even from her enemies: thus we may facilitate alliances, as we shall see in Part IV, Chapter I, No. 5.

The pump of the ♀ seminal vesicle, the dimensions of which are exactly adapted to the size and duration of the colony by the number of its inhabitants and the longevity of the fertilized ♀, is a splendid example of the hereditary adaptation of an organ to the needs of social life. I have described this organ by the term 'secondary hermaphrodite.' It is really hermaphrodite in the sense that a female which fertilizes her eggs herself has ceased to be purely ♀; she has *become* hermaphrodite. But when she was a virgin she knew the pleasures of love for a day—hers was even a poetic and aerial love-affair.

There is nothing repulsive about this innocent polyandry, which is quite natural and adapted to social needs. Only the unwholesome eroticism of men could raise a sneer at the thought, coupled with hypocritical blushes. And afterwards, when she has rid herself of wings which are now useless, our ♀ in her prison becomes a peaceful secondary hermaphrodite, whose sole task is to lay the greatest possible number of eggs, which she fecundates proportionately with great economy.

Janet has proved that the wing-muscles, which fall after the fertilization of the ♀, are reabsorbed by the blood, and therefore serve indirectly to nourish the first children of the future mother. This is a fact of physiological, utilitarian and social adaptation—as important as it is interesting.

But the most interesting social pump is that of the pharynx, which pumps into the swollen crop nearly all the honey-dew which the ant gives freely to her community. Nevertheless, let us not exaggerate the social *virtues* of the ants; thanks to the organ of taste, Nature, by adaptation, has undoubtedly rendered the regurgitation of honey-dew very agreeable. We need only look at the figure on our cover: the regurgitating ant with her backward-flung antennæ has a look of ecstasy, and undoubtedly feels as much enjoyment as the one which is swallowing. And the physiological process of swallowing and regurgitating is interrupted only by social work, rest and warfare. It is being repeated every moment in the life of the ants.

In describing the combs and brushes on the ant's legs and mouth, as well as her tongue, mandibles, jaw and spur, we pointed out the ceaseless cleansing function which is characteristic of these organs. They serve to clean not only the body, and the antennæ in particular (fig. 78, Part III), but even the eggs, larvæ, nymphs and cocoons. Ants are eminently clean, and their cleanliness is partly responsible for preserving them and their brood from the mould, and the microbes and parasites which pursue them relentlessly and threaten the existence of their colony.

Some of the ant's glands have individual functions, like the salivary and rectal glands, etc. Others have social functions, like those which glue together the fragments of carton and those of the larvæ which are used as weaving-shuttles; others again, such as the poison and anal glands, are used in defensive and offensive warfare. We shall return to these in Part IV.

But here a few remarks must be added. Not to speak of the glands with oily secretions, which are licked up by certain parasitic guests and even by certain other ants, it is undeniable that some of our little friends give out a specific smell. Most of the *Dolichoderinæ* do this only by means of the powerfully aromatic but momentary secretion of their anal glands (*Tapinoma* odour). The *Formicinæ* ejaculate formic acid, with a faintly acid smell, from their poison glands. But other species exhale a definite odour, generally fetid, which is peculiar to each

Examples are *Dendrolasius fuliginosus*, *Lasius emarginatus*, certain American *Lasius* and *Paltothyreus tarsatus*, a Ponerine species with a fecal odour.

In the *Bulletin de la Société entomologique de Belgique* (Vol. III, No. I, February, 1921, p. 24), Stumper has published some interesting chemical and biological studies on the secretions of a few ant glands and their smell, especially that of the poison glands. The proportion of formic acid is very large in the *Formica* of the *rufa* group and in *Camponotus ligniperdus*, small in *Lasius* and a few other *Formica*, and nil in the *Myrmica* and *Dolichoderinæ*. Stumper considers that the *Tapinoma* odour is due to methylheptenone, and that of *Dendrolasius* to trinitopseudobutyltoluene. Verily, chemists do confront us with some monstrous names! It is to be hoped that Stumper will continue his studies, for this field is still untouched. He has reduced to absurdity the imbecile hypotheses advanced by Henning of Frankfort, who thinks that he can explain the orientation of *all* ants by the traces of formic acid.

The muscles of ants, as we said in the Anatomy section, are all striated and hence adapted to rapid motion.

It would be well to look at figs. 8, 26, 27, 28, (Part I), in order to understand the acrobatic feats and the relatively incredible strength of these little insects, which lift and carry, without any difficulty, burdens ten or twenty times as heavy as themselves. The last mentioned figure (28) shows the strong muscles of the head which move the mandibles; but this showed an ordinary species, which has no heavy weights to lift. In the large ☿ of *Messor*, *Atta*, *Pheidologeton*, and the ♃ of *Pheidole*, the strength of the muscles surpasses belief, and it is by their means that ants succeed in triturating seeds with their mandibles or even in cutting with a single bite through the hard, horny skin of the human finger, until they draw blood, as the *Atta* did to me when I was destroying their nest in Colombia. These same *Atta* cut through even the very thick leaves of the tropical trees with their mandibles alone, as we cut bread with a knife, and as fig. 114 (Part V) will illustrate. In a word, so far as muscles are concerned the ants are diminutive Titans.

In the chapter on Internal Anatomy we described the muscles of the internal organs and their action, particularly those of the gizzard, the poison glands and the heart: we shall not deal with them again. It is chiefly to the Russian naturalist Nasonov that we owe a patient and detailed study of the muscles of ants.

But the muscles are only *mobile instruments*, utilized for their action by the ganglia and the nerves, by means of conducting threads represented by nerves. The brain, ganglia and nerves are motionless, but they electrify the muscles and thus cause the ant to move. In the same chapter on anatomy in Part I, we have depicted the nerves and the brain of the ant. As in our own case, there is no clear-cut limit in the ants between the most primitive nervous functions, known as reflexes, and the highest functions of the mind, which are said to be 'conscious.' In them, as in ourselves, everything is gradual.

What is a reflex? If a doctor strikes with his hand or a small hammer the tendon of our patella when the leg is hanging loose, we make unconsciously, and against our will, a sharp movement with the leg; this is a reflex. Our heartbeats are automatic reflexes. It is the same, usually, with our respiration, though this can be voluntarily stopped for a moment, and hence it forms a first transition. And there are many other examples. Practically the same thing obtains with the ants. If they are deprived of their brains, they are capable of scarcely anything but reflexes —either short, as, for example, in the irritated nerve of a single leg which has been severed, or longer and more complicated, as in a body from which the head has been cut off. The reflex, in a word, is a movement caused by the irritation of a nerve, whether direct or produced indirectly but immediately from that of the ganglionic cells, without passing through the main centre of the brain.

Having said this much, before we go any further we must explain what Huber first described as the 'antennal language' of ants, which is represented in fig. 75 (Part III). Here we have a language which is fundamentally instinctive but highly modifiable according to circumstances. This language possesses a topochemical vocabulary scarcely less rich than the song of birds. The Jesuit Father Wasmann, whom no one could accuse of wishing to make ants into human beings, has devised the following vocabulary, among others, from their antennal language:

1 It is above all an incitement to collective work, passing from one individual to the other.

2 By caressing and lightly tapping a companion with her antennæ, one ant begs and implores the other to regurgitate for her a little honey-dew.

3 By striking a companion sharply with her antennæ and afterwards moving away in a certain direction, an ant that is about to move her quarters invites this companion to follow her to a new nest.

4 In a very similar way, an ant which has somewhere discovered a source of food invites her companions to follow her to such a place.

5 By violent blows with the antennæ, often delivered

with her mandibles open, an ant urges her companions to the attack, or, on the other hand, to flight.

6 Blows are often given with the antennæ by an ant which wishes to warn a companion of a danger coming from a certain direction.

7 By friendly antennal caresses, constantly repeated, ants endeavour to calm the affective excitement of one of their companions.

8 Slave-making ants give their companions the signal for departure on an expedition by rapid blows with the antennæ or head. In the same manner they point out to them a change of direction as soon as hesitation or stoppage has occurred on the march.

We may add that the 'state of mind' of ants is very visibly shown by the calmness or violence and rapidity of their movements in general. Discouragement is often expressed by the momentary abandonment of the nest and brood. When they are driven to despair by the continuous destruction of their work, this discouragement may lead them to deteriorate until they devour their own larvæ and abandon everything. According to Brun's statements, which I have always been able to confirm by my own observations, the difference between the various signs of the antennal language lies chiefly in their violence or calmness, their lightness, and their length or shortness, with the frequency of the pauses between them. These signs also differ according to whether they are struck on the forehead, the sides of the head, the body or the antennæ themselves of the companion to which the ant addresses herself. There are also many transitions between these various signs. Needless to say, the nature and form of smells likewise plays a large part in antennal language. It is only by long and patient observations that we men can achieve an *approximate* reading of this interesting ant-language. Two examples may be given:

Lubbock often used to pin freshly-killed insects on to a piece of cork and leave them to be discovered a fair distance away from their nests by a single ant of one species or the other. The ant strove in vain to carry away the body. She unwillingly went off, but soon returned with several friends which she had informed and brought to her aid. Their united efforts then succeeded in cutting up the corpse where it lay, in order to carry it away in pieces.

In the refuse-chamber of an artificial nest of *Formica sanguinea*, Wasmann had placed cocoons of *F. fusca* and *rufibarbis* while no ants were present, and these cocoons remained there for an hour and a half without being perceived. Wasmann then took a single *sanguinea* ☿ and placed her near the cocoons. After a moment, she ran to the upper nest, crossed it without stopping, and passed through the ante-chamber to reach the principal nest. Scarcely had ten seconds elapsed before a horde of *F. sanguinea* ☿ came out of the main nest, crossed the ante-chamber and the upper nest, and after hesitating for a few seconds only, betook themselves to the refuse-chamber, where they began to carry away the cocoons to the main nest and afterwards continued to do so all the afternoon. This experiment needs no comment. If my readers wish to grasp its full significance, I beg them to turn to the first chapter of Part III, 'Observation Apparatus,' in which Wasmann's nests are described.

Again, as Huber has already shown, ants do not talk exclusively with their antennæ. Particularly when they are excited, they strike the bodies of others with their heads. When they are asking for food, they also caress with their front legs the companion which is regurgitating honey, somewhat in the manner of dogs. When a companion which has been warned of a danger, or which has to be transported, turns "the deaf ear" they seize hold of her by the legs and drag her away. The *Camponotus* in their wooden nests strike the walls with the abdomen and the head to signify danger; I have seen and heard them do so many times, for this noise is clearly perceptible to the human ear.

We come now to the functions of the ant's brain—in other words to its psychology, its mind, to which we shall have to return again and again. In the introduction to Part I, we have already said a few words about Semon's 'mneme,' about the engrams which are left by all sensory and other irritations in living organisms, about their conservation and their *ecphory* or revivification by *memory* in the individual and by *instinct* in *heredity*, and lastly about the hereditary instinct itself, compared with all that the individual acquires during his life, that is, throughout his whole ontogenesis from the egg-stage till death. Weigh carefully in your mind, friend reader, the importance of this, for it is at the very basis of the life of body and mind in plants, animals and man. I have also mentioned the secondary *automatisms*, which in the individual are the result of the ever-repeated ecphory of certain engrams, and which thus form *habits*. These habits fall back into automatism, becoming unconscious or rather sub-conscious, in us human beings at any rate, and undoubtedly also in the higher animals and even in the ants.

And now you will tell me that I am contradicting myself and trying to make ants into human beings! Not at all—comparison and identification are two different things! Allow me, therefore, to make a comparison. You know the story of Panurge and his sheep: when their leader was thrown into the water all the others followed. A strong leader draws the majority with him and then the minority can but follow, in men as in sheep. Have we not just seen that ants do the same thing by means of their antennal language? Nevertheless a single sheep, a single ant, above all a single man, does not *always* succeed in drawing the majority after him. There are minorities which are able to put up a resistance, especially among those men who are capable of thinking and willing on their own account.

We will now assume, at what risk is matters not, that the engrams acquired during the life of man by study, by books and most of all by well-reasoned and laborious reflection, constitute *on an average* 60 per cent. of his thought and will, and thus also determine 60 per cent. of his actions. I fear, indeed, that this figure may be too high. The rest is due to hereditary dispositions, to constellations of instinctive passions and to the imitative prejudice in favour of the acquired routine followed by the unreflecting majority. We will assume on the other hand that in the ant, instinct fixed once for all by heredity constitutes alone 95 per cent. of the thought, will and action. To these we may add 4 per cent. due to emotional constellations and the routine of habits fairly rapidly acquired (secondary automatisms). Even then, 1 per cent. still remains for reflection, which can modify the ant's actions according to circumstances and special cases.

One per cent., forsooth, is very little; such a trifling fraction can only be perceived by close attention and much perseverance on our part. That is why it is missed by the majority of those human beings who look at ants, and also why this same majority regard insects as mere machines, whereas they consider themselves to be created in the image of God. I really do not think I have exaggerated anything or committed any error in my comparison, summary as it may be.

We have already proved memory in ants, especially in describing experiments on their topochemical smell. With bees and wasps, it is much easier to prove visual memory in their flight; I have even managed by this means to prove a memory in bees not only for places but for time, for whenever they had found jam once or twice, even though such things were no longer put on the table, they always came back and were found again at the time and place allotted for our meals. In ants, it is more difficult to prove as much for sight; but it is also shown by the experiments of Santschi and Brun with the sun. Moreover, all the habits of the ants, which we have still to discuss, are full of proofs of their memory, especially topochemical memory, for places and 'persons'—that is, other ants.

Individual memory acquired in the course of life, in other words, the sum of the engrams acquired and combined with each other, and capable of combining with the hereditary instincts, this memory or mneme, I repeat, constitutes the basis of all reasoning, in ourselves as in the ants. When an ant instinctively *seeks* or *avoids* something and *discovers* the *object* she has been seeking, or a place of *shelter*, she desires, still instinctively, to inform her companions. But in order to do so, by means of the signs also instinctively inherited in the antennal language, she must not only *find* her way again but also *lead* her companions thither, either by carrying them or by making signs. It is here that acquired memory comes in. The best proof of this lies in her *doubts*, *hesitations and mistakes*, particularly clear in the expeditions of *Polyergus rufescens*, of which we shall speak in Part IV, but also in the above-quoted experiments. The ant *corrects* her errors. She does this by comparing the sudden quandaries in which the experimenter may happen to place her, or even a haphazard situation unforeseen by *instinct*, with the *memories* she has personally acquired of places and of her *companions*. It is then that flashes of reason are produced.

For example, an ant which is fleeing after defeat or which has been turned out of a bag along with her companions and her brood in an unfamiliar place may chance to discover a shelter, suitable for her distressed colony. She turns swiftly to her companions and seizes one of them, or a cocoon, to take it into shelter. But she has had no time for thorough orientation. Once she has a burden, she sometimes loses her bearings. She then lays down her burden for a moment and tries to find the way by means of her antennæ and her sight. At last she finds it and once more picks up her companion, who unfolds her legs and waits patiently, or else her motionless cocoon. Her companion offers no resistance and folds up her legs afresh, and thus they reach the shelter. The companion which has been carried then examines the shelter, and usually hastens to imitate her bearer, and so forth. But when any ant has discovered a shelter better than the former one, the majority soon abandon the less favourable shelter and transport their companions and their cocoons to the better shelter. How are we to explain all these facts without memory, or without the hypothesis of actual combinations between the ecphorized engrams and instinct?

Obstinate pedants who think to explain everything by 'reflexes,' 'tropisms,' unknown forces, or some other big words, are simply stopping their ears and throwing dust in the eyes of their readers, instead of observing with perseverance and attention, and experimenting the while. Do not imitate them, dear reader, but check all that I tell you yourself.

Wasmann succeeded in taming a ☿ *F. rufibarbis* to such an extent that she would come and eat off his finger.

In 1907, Turner trained some *Myrmica* and *Formica* so that they would fall from the height of a platform, carrying a nymph, and then bear it to their nest. These ants allowed him to put them back on the platform with a brush and to repeat this performance several times.

Turner taught a *F. subsericea* to use a small movable bridge, made in sections, to pass from a platform to the nest, which was in the form of an island. His experiment is as follows:

"I took at the same time two ☿ marked *A* and *B*. *A* quickly found the way, which led down indirectly to the island by an incline beneath the platform, but *B* could not find it: she ran about the platform at random, vainly seeking a passage on the level of the platform, from one corner to another. I tried to push *B* in the right direction, towards the slope, but in vain.

Struck by a new idea, I pushed the little bridge underneath the ant and thus transferred her direct to the island. The ant then walked along and carried her nymph to the nest. As soon as *B* came back from the island, I pushed the little bridge under her again and transferred her to the platform, whence she set out to pick up another nymph. I then transferred her anew to the island with the bridge. After I had repeated this performance several times, *B* would remain calmly on the bridge as soon as she was put there, and would not move while travelling in either direction until she landed. She immediately climbed on the bridge, whether to carry a nymph to the nest or go in the opposite direction to look for another: in two hours about fifty of these to-and-fro journeys had taken place.

When I offered the same bridge to the other ☿ from the nest, even to *A*, they attacked it, avoided it, or bit me. *A* and *B*, therefore, gradually learned to perform the same actions, with the same end in view, but in two different ways, so that eventually what attracted *B* was repugnant to *A* and *vice versa*, owing to their different personal experiences."

But on the other hand, do not forget the important differences between the sensations of ants which I have pointed out to you. It is these and their memory which provide us with the principal key to all we have most difficulty in understanding in connection with their habits. We have seen, and shall see on every future occasion, the stupidity of the ♂ relatively to the ☿. This stupidity corresponds to their lack of memory, reflective power and brain; they are instinctive machines to a much greater extent then the ☿. All the same, they vary in intelligence according to species. The most intelligent species I know, the most adaptable and capable of modifying its actions, is our ☿ *Formica sanguinea*. Our *Ponera coarctata* stands at the other extreme and seems to be very limited.

This brings us finally to the brain, described in Part I, Chapter IV, in other words, to the organ of 'the ant's mind.' In an experiment of first-rate importance, I proved that ants which have been cut in two with a razor behind the pro-thorax conserve all their intelligence and all their memory in the head, and that they have a clear recognition of their companions, enemies, etc. Even the head by itself certainly appears to be similarly circumstanced, but in the absence of sufficiently extensive movements it is more difficult to prove this. On the other hand, an ant's body with the head cut off can only make aimless reflex movements. It follows that the brain—that is, the *pedunculate bodies*—centralize and co-ordinate all those movements of the body which are capable of carrying out a design. Consequently this same organ is also the organ of the memory, the social habits and the small reflective capacity possessed by our tiny friends. I have proved that an oblique hermaphrodite *P. rufescens*, which we shall mention later on in Chapter V, and whose head was entirely ☿, though its abdomen was almost completely ♂, was able to take part in a slave-hunting expedition, and itself carried off a larva, which it took back to the nest—a feat which even the ♀ cannot accomplish. This is surely clear enough !

There is no need to dwell upon such well-proven facts, which will be confirmed by all the remainder of my book: the plastic mind of the ants resides in their brain, as ours does in our brain. We may add that the cases of brain-piercing in *F. rufibarbis* by *P. rufescens*, such as are represented in fig. 106, *A*, *B*, *C* (Part IV), generally end in a simple automatic stupefaction of *F. rufibarbis*, like that of the ants which have their entire heads cut off. And as a rule, at any rate, it can scarcely be anything but the pedunculate bodies which are pierced in these cases and more or less destroyed.

Chapter III

ANTS AND PLANTS—SYMBIOSIS—SYNDIACONY

As I do not wish to encroach upon Part V, which will deal with many of the special relations between ants and plants, we will confine ourselves here to general facts. Generally speaking, plants can dispense with animals, whereas animals can only live by eating plants or other animals. But if they were to eat each other only, animals could not develop their species. Hence, directly or indirectly, it is always the plants which ultimately nourish them—indirectly when a carnivorous animal feeds on herbivorous or frugivorous animals, which is very commonly the case.

Deserts are very instructive in this respect. At a first glance, it almost seems as though the only spectacle they present is that of animals mutually devouring each other. But here and there we notice small plants, grasses and others, in most cases covered with spines, but always browsed upon by camels, asses or gazelles. Their seeds are also plundered by the harvesting ants, especially by *Messor arenarius* in the Sahara, by *Pogonomyrmex* in the American deserts, etc. True they are very meagre, but they grow all the same, and are fed by the excrement of numerous animals.

Except for a few essentially carnivorous groups, therefore, such as the *Dorylinæ*, *Machæromyrma*, *Leptogenyini* etc., ants may everywhere be seen adapting their nests and their habits to plants. Consequently the ant fauna varies according to the nature of the plants among which they live. There are prairie species, forest species, steppe species, desert species, species adapted to the hollow, dry stems of brushwood, where they nest, species which gnaw wood and others which inhabit hollow trees, species which nest in spines, in bamboos, in gall-nuts, and even under or between leaves, etc. Many ant nests are built on trees out of carton, and others inside their trunks.

By *symbiosis* (life with) we mean the more or less constant and intimate union of one species of living beings with another species. The term *integral* or complete symbiosis may be used to distinguish those in which neither of the two living beings can actually exist without the other. Cases of this sort are rare, and can only be explained by their ancestral phylogeny (see Part I, Chapter I). Ants of the *Attini* tribe with their fungi provide an outstanding example. We shall discuss them in Part V, and we therefore need not describe their history here.

Much more frequent are the *partial* symbioses, which are of two kinds. In the first, one species is absolutely dependent on the other or on several others, which in their turn can do without its aid. This form of partial symbiosis forms a gradual transition to a more or less accentuated parasitism of the dependent species upon the other; but there are cases of partial symbiosis in which the two living beings nevertheless render each other mutual services. In the second kind of partial symbiosis, the two species can do without each other more or less easily, but they render each other so many mutual services that this is the exception. Here again, all possible transitions are found.

Furthermore, three kinds of symbiosis may be distinguished, especially in ants:

1 Between two different species of ants. Of these we shall speak in Parts III and IV.

2 Between a species of ants and other animals. We shall speak of this in the next chapter.

3 Between ants and plants. This is our present theme.

Partial symbioses between ants and plants are very numerous. Generally speaking, it is the plant which provides the ant with its nest, and sometimes also with food; whereas the ant defends the plant from animals which are harmful to it. I will cite a few examples:

Certain Indian plants known as *Myrmecodia* and *Hydnophytum* have at their base an enormous bulb pierced throughout the interior by a whole labyrinth of channels and cavities, as represented in fig. 64. This labyrinth is nearly always inhabited by little ants of the genus *Iridomyrmex* (*I. Myrmecodiæ*), and sometimes also by other ants, such as *Camponotus*, to such an extent that some writers have supposed it to be carved out by the ants. But Treub of Java has proved that the bulb of *Myrmecodia*, etc., is produced with all its labyrinth by the plant alone, and is naturally hollowed out from the beginning; and that the plant is able to live and develop completely without having ants in its bulbs. This does not mean that the ants are not adapted to it and do not protect the plant to a greater or less extent; *I. Myrmecodiæ* is not found anywhere except in the bulbs of *Myrmecodia* and *Hydnophytum*.

A whole genus of plants and trees, *Triplaris* of the American tropics, whose leaves are frequently cut by ants of the *Attini* tribe, have the centre of their branches and trunks naturally hollowed out by passages; and several ant-species of the genus *Pseudomyrma* have specially adapted themselves to *Triplaris*. They regularly inhabit the central passages of the stems (see Plate VII *d*), defend their trees violently and sting every creature that attacks them. I felt their stings on my own skin in Colombia, when I discovered the *Pseudomyrma* which I named *symbiotica*. The whole tree was green, but a small dry branch at its base must have served as an entrance to the ants populating all the central passages of the green branches. At my request some Indians cut down the tree with their hatchets, which enabled me to examine it thoroughly.

Fritz Müller's famous Imbauba ant of Santa Catharina (Brazil) *Azteca Mülleri* lives in the same way, as is shown in fig. 61, inside the branches of the tree called *Cecropia*, where she builds the nests of carton. Müller has proved that she lives mainly on certain nutritive corpuscles secreted by *Cecropia*, and that the fecundated ♀ take advantage of a small narrow space in the bark of the tree, situated between each node and the stem, to work their way in and found the colony there. Müller looked upon this as complete symbiosis, in which the ant always protected the tree against the leaf-cutting *Attini* and other enemies. But Ihering and others have proved that *Cecropia* does not harbour *Azteca* in its earlier stages of growth, that often there are no *Azteca* in the region where it lives, and finally that the *Azteca* do not keep off the plants' worst enemies. Nevertheless, Ihering has grossly exaggerated things in his systematic and heated opposition. On the side of *Azteca*, symbiosis is complete and successful, and the plant does not suffer in any way, rather the reverse.

Many plants possess what are known as *nectaries* either in their flowers or outside them, which secrete a sweet liquid, the 'divine nectar' of the ancients; or, in other words, the substance from which bees make their honey. When they suck the nectar, bees and ants fertilize the flowers at the same time by brushing against the stamens. This is another reciprocal service between insects and plants.

Many species of *Azteca* and *Pseudomyrma*, etc., are adapted to the cavities of certain plants—*Tococa*, *Cordia* and others—which supply them with nests and sometimes with food; whereas the services rendered by the ant to the plant are more or less problematical, and vary with the circumstances.

A remarkable ant, *Camponotus* (*Myrmomalis*) *mirabilis*, whose head is represented in side and front view in fig. 30, is completely flattened and certainly lives between two surfaces a small distance apart from each other, probably under the bark of a tree, in the same way as *Azteca polymorpha*, which it resembles: but nothing is known of its habits.

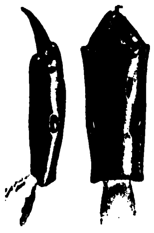


Fig. 30

I myself discovered in Colombia a small new *Azteca*, *A. hypophylla*, whose large ☿ has a flat head. It lives under the round leaves of a climbing plant which encircles the bark of certain trees in the virgin forest. These leaves cling to the bark of their own accord. *A. hypophylla* contents herself with completely closing the narrow space separating the bark from the edge of the leaf, by means of carton which she makes with the aid of her saliva, and her nest is ready for her. This is all the mischief that is done. A small lateral hole left in the carton serves as a door by which *Azteca* can come out, and several of the 'nests' which she thus forms constitute a single formicary in a minute *polycalic colony* (colony with several nests).

Many ants live in the spines of acacias and other trees, in which they devise a small irregular opening, unless another insect has done so before them. There they occupy the cavity of the spine, which is sometimes swollen at its base, and this cavity constitutes their entire nest; but their colony is often polycalic on a single tree. Certain species are adapted in partial symbiosis to certain forms of acacia, especially in tropical America and Africa; as is shown in Plate VII, figs. *a* and *b*. In fig. *a*, a nest of the American *Pseudomyrma spinicola*, the whole spine is swollen; in fig. *b*, a nest of the African *Cremastogaster Chiarinii*, it is only swollen at the base. In the case of the *C. Chiarinii*, the cavity of the spine contains small chambers made by the ants out of carton. There are also other spines which have their bases swollen, but full of wood, like those of the plant *Erythrina umbrosa* in the Island of Trinidad, In this base, *Procryptocerus spiniperdus* hollows out her nest with her own mandibles, as shown in fig. *c*, Plate VII. It is difficult to say where partial symbiosis begins or ends. Belt has shown that certain acacias have nutritive nectaries at the ends of their leaves, to attract the ants in the same way as Müller's corpuscles attract *Azteca Mülleri*. Furthermore, the Swedish naturalist Sjöstedt has proved that *Cremastogaster Chiarinii* resolutely attacks any animal—antelope, gazelle or insect—which attempts to attack the acacia in which it lives. It is adapted to this tree, which is known as the *fluted Acacia*, so called because the wind whistles with a flute-like sound through the holes which *C. Chiarinii* has made in the spines. The carton comes from the dried remains of the spongy mass which filled the spines before the ants found their way in. This, therefore, is certainly a case of mutual service, if not of integral symbiosis. We must not exaggerate one way or another.

A very small Indian ant with a wingless ♂, *Cardiocondyla Wroughtoni*, nests in a single leaf between the two layers of cells separated from each other by a small gnawing worm. In this diminutive nest lives the entire colony, ♀, ☿ and ♂; the whole lot have been sent to me. Here it is plain that the ant alone has adapted herself and has taken advantage of the plant.

In order to give my readers an idea of the frequency of these partial symbioses, I should like to mention briefly a few examples.

Out of the spines of various acacias, I have received from America *Pseudomyrma Belti*, *subtilissima*, *spinicola*, *nigrocincta*, *acanthobia* and others; from Africa *Cremastogaster Chiarinii*, *Acaciæ*, *Ruspolii*, *castanea* v. *simia*, *etc.* These species or varieties seem to be adapted to the spines of acacias.

From the hollow interior of the stems or trunks of the tropical American *Cecropia* we obtain among others the following species living in partial symbiosis (complete only for the ants): *Azteca Mülleri*, *Emeryi*, *constructor*, *cæruleipennis*, *minor* and *Alfari*; the last with numerous races and varieties, all found in the *Cecropia*, where I have taken it myself; besides *Camponotus Ulei*.

In swellings in the stems of *Tococa* we find among others *Azteca depilis*, *Traili* v. *tococæ*, *Allomerus octoarticulatus* and *Pheidole minutula*. Here symbiosis seems to be more doubtful.

In the hollow stems of *Triplaris* of tropical America are *Pseudomyrma dendroica*, *Triplaridis* and *arboris-sanctæ*, whose symbiosis is the same as that we have just witnessed in *symbiotica*.

In the swellings or galls of plants of the genus *Cordia*, the following American forms live in symbiosis: *Pseudomyrma* *sericea* v. *Cordiæ*, *Chodati*, *Azteca Stanleyuli*, *A. longiceps* race *cordincola*, *A. Pittieri* v. *emarginatisquamis* and still others, which seem to be adapted to the *Cordia*, that is, to their galls.

In the swellings and cavities of *Duroia* we find *Azteca Duroiæ*, *angusticeps* and *depilis*, as well as *Allomerus septe-articulatus*, which appear to be similarly circumstanced. In the swellings and branches of *Coussapoa* we find *Azteca Coussapoæ* and *Pseudomyrma Ulei*. In the swellings on the leaf-stems of *Tachigalia* dwell *Pseudomyrma Tachigaliæ* and *Azteca Tachigaliæ*. All this shows a very uniform tendency to partial symbiosis in American ants.

In the green stems of a plant, Tonduz discovered in Costa Rica the only lustreless greenish ant known to me —*Azteca virens;* he also found *Azteca Tonduzi* in the bulb of a plant belonging to the *Orchidaceæ*.

Certain ferns of the genus *Polypodium* have tubercles analogous to those of the *Myrmecodia*, in which dwells *Azteca filicis* of Peru. According to Dahl, *Camponotus* (*Myrmamblys*) *quadriceps*, in the Bismarck Archipelago, inhabits the stems of *Endospermum formicarum*, whose leaves, as we see in fig. 66, provide it with corpuscles analogous to those discovered by Müller. *Myrmelachista Ulei* inhabits the swellings in the flowers of *Pteroclada*, and *Solenopsis amazonensis*, the onion-shaped cavities of *Tillandsia*. Finally, *Azteca Schumanni* is found in the vesicles of *Chrysobalanea hirtella*. I could add still other examples, but these are enough.

The reader must forgive such a heap of Latin names, but they are intended to prove that we are dealing with particular species adapted to this or that plant, not with superficially generalized hypotheses. The future surely reserves numerous surprises for us in this respect.

We now come to the second kind of partial symbiosis mentioned at the beginning of the present chapter, in which ant and plant render each other mutual services, yet can do perfectly well without each other. I might call this *syndiacony*, or better, 'mutual service,' were I not a trifle afraid of increasing still further the number of special terms. My excuse would be that the following facts show too much divergence from what we understand by symbiosis to be classed under it without any qualification.

Lincecum and McCook observed in Texas what is known as the 'harvesting' ant, *Pogonomyrmex molefaciens*, which collects, in particular, the seeds of certain Gramineæ, *Aristida obligantha* and *stricta*. They noticed that in the immediate vicinity of the nest, this ant cut off all other plants except *Aristida*, and hence they thought that she cultivated it specially. Since then, Wheeler and others have shown that there was nothing regular and deliberate about this proceeding, but that it simply followed from the fact that the remains of the seeds which had germinated too soon and been rejected by the ants were growing and propagating themselves especially well in the region just round the nest. However that may be, it is evident that granivorous ants in general transport seeds, and thus often sow them with or without 'cultivation.' Here, therefore, we certainly have a case of mutual service or syndiacony.

Sernander has given the name *myrmecochores* (favourite food of ants) to certain seeds with oily appendages which serve to attract ants towards them or towards their fruit, and thus to secure transportation by these insects. It is chiefly plants and bushes growing in the shade of the forest and hence deprived of transport by wind or birds which have need of *myrmecochorous* seeds, so as to be sown and spread abroad by ants. In this connection Sernander has made innumerable comparative experiments on the seeds of various plants. For instance, he mixed seeds of an indifferent character with ten others belonging to a plant suspected of *myrmecochory*, and placed them on an ant-track; he then noticed the time the ants took to transport the second kind, while they entirely ignored the first. He also observed the relative number of seeds carried, the distance covered and the abandonment of certain seeds by the ants on their way. Thus he succeeded in finding 80 myrmecochorous plants in oak-forests, 45 in beech forests, but only 16 in forests consisting of birches and still less in those consisting of pines. Sernander calculated that a single colony of *Formica rufa* has thus transported at least 30-480 seeds in the good season of the year (I am quoting from Escherich). These patient researches, summarized in a volume of 200 pages quarto, leave no doubt as to the syndiacony of *F. rufa*, *Lasius niger*, etc., with the flora of forests, in accordance with their denseness.

Moreover, Ratzeburg had earlier proved that the trees of forests which overshadow a colony of *F. rufa* are preserved like so many oases from destruction by the bark-beetles and other coleoptera which ravage them. Hence in Germany the destruction of these nests has been strictly forbidden by order. I have myself counted by the minute the number of insects, grasshoppers, caterpillars, worms, etc., killed and carried away on a single track belonging to some *Formica pratensis* whose nest was situated in a meadow near a hedge. In summer, seven such tracks were in use day and night. I counted four insects a minute on an average, which means that about 40,000 insects are thus destroyed every day. I am persuaded that here again the syndiacony of these ants with the plants and trees of the meadows and forests admits of very little doubt. On the other hand other species of ants are extremely harmful to plants, as we shall see later on—chiefly on account of the rearing of aphids.

As early as the XIIth century, the Chinese reared and protected certain ants to destroy the caterpillars which ravaged their orange and mandarin plantations. Raciborski even says that a class of workers called 'ant-gatherers' was formed in China for this purpose. The same author also tells us that the Japanese learned long ago to protect the fruits of their mango trees against a destructive beetle by the aid of a very aggressive red ant, which they pick up and take into their gardens for this purpose. Similar examples in other countries have been cited—at Mantua in Italy, for instance. In Texas, *Solenopsis geminata*, or the American fire-ant, so named on account of its painful sting, is highly valued for its usefulness in destroying the beetle and its larvæ and nymphs which ravage the cotton-plantations. It has been calculated that the *S. geminata* destroyed as many as 50 per cent. of these terrible larvæ alone.

The same thing obtains, especially in Africa, with the *Dorylinæ* or visiting ants, which destroy in their hunting expeditions all insects within a range of some hundreds of yards, and then emigrate to a distant region. Vosseler, who has observed them for years, considers them a veritable blessing to various crops. He estimates the number of insects devoured in ten days by a single colony of *Anomma* over a surface of about 10,000 square metres as 1,600,000. Escherich thinks that *Anomma* and *Dorylus* will probably play a very important part in the future of tropical plantations in Africa.

This brings us to a consideration of a general character. When man selects for his own profit animals or plants from which he thus breeds special varieties adapted to certain uses, or to his food, he has in view his own interest solely, and not in any way that of the animal or plant he selects. As a result, instead of strengthening the faculty of resistance to natural enemies in the living being which he thus reduces to slavery, he weakens it. This artificial selection, in a general way at any rate, works in an opposite direction to natural selection. We have only to look at one of the famous English pigs, which have ceased to be anything more than bundles of fat, almost incapable of moving.

The result of this state of affairs is that all the living plants and animals which have been submitted to man's artificial selection are less resistant to diseases, parasites and their natural enemies in general, than the creatures we describe as wild. Those who rear plants and animals are beginning to perceive this more clearly, and hence they are striving their utmost to increase the resistance of the races they select. The struggle, therefore, between man, who desires to extend his crops and his domestic animals to all parts of the world, and wild creatures is constantly growing more bitter. We are unable to modify any of these factors. We have just seen how the opposite is sometimes brought about in mutual service—in *syndiacony*. Here we human beings can utilize to our advantage the services which ants render to plants, like deacons or servitors, without disturbing thereby their selection, nor their mutual relations, which are quite natural, simply by lending a little assistance to the species which is most useful to us.

Plants are useful to ants in yet other respects. There are many which they use in constructing their nests, or by dwelling on or in them, whereas others are indifferent to them, as they have neither nectaries, nor utilizable fats, nor special cavities. But there are also plants which injure

Nest of *Gremastogaster* (*Oxygyna*) *Emmæ*. Madagascar. Original photograph.

ants. Here I may mention, more as a curiosity than anything else, the insectivorous *Nepenthes* of Ceylon, which swallows and digests ants among other insects, even a very rare ant, *Aneuretus Simoni.* By reason of its sting this ant forms a transition from the *Dolichoderinæ* to the *Ponerinæ.* Günther once sent me a specimen imprisoned and half digested in the closed corolla of *Nepenthes.*

Much more seriously harmful to ants, however, are the various mosses, and particularly *Polytrichum* and *Sphagnum*, which are represented in Fig. 31, *Polytrichum* by *P* and *Sphagnum* by *Sph.* These mosses infest many ant-nests, especially in marshes, as described by Holmgren. *Polytrichum* infests the bottom of the nest and forces the ants to emigrate farther and farther towards the summit, where their colony vegetates and gradually diminishes to such an extent that in the end it occupies no more than the part denoted by *nid* (nest) in Fig. 31. But at this juncture the *Sphagnum* arrive, to replace and destroy in their turn all the *Polytrichum.* Finally nothing remains but a round hillock, void of ants but covered with *Sphagnum*, to bear witness to the fact that a disused formicary once reared its dome on that site. Other mosses also destroy the nests of certain ant-colonies in a more or less similar fashion, as I have myself observed.

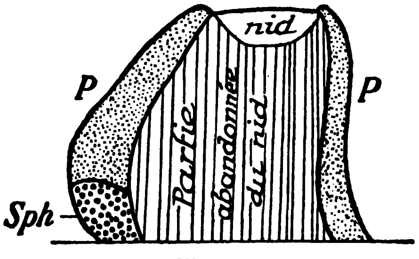


Fig. 31

A few more words by way of concluding this chapter. As Darwin has clearly shown, life consists of a huge struggle without truce or respite, between one living being and another, in the course of which inanimate matter is also exploited. It is useless and idle to ask why; the fact is there. But this struggle may be individual or social. Between the female spider, which devours her male after mating rather than lose anything, and the ant which lives, fights and works for her colony alone, there is a difference. Everywhere in the course of this struggle we find alliances, individual and also social. There are plants which eat other plants or live on them as parasites, but there are other plants which form associations among themselves, as many animals do.

And as we have just seen, the same phenomenon is reproduced between the two great kingdoms of life, the plant and the animal. As ants are social, they possess a 'social character,' symbolized by symbiosis and syndiacony; struggle on the one hand and mutual aid on the other between plant and ant. Seeing that there is no true morality on the earth—which contains all the life known to us—other than this social and entirely relative morality, let us turn to it joyfully and profit by it.

To do this much, in the first place we must imitate the ants in all that concerns their social inter-relationships in the colony: this will teach us to make a 'second nature' of social work in our own sphere. In the second place, we must refrain from imitating them in their warfare, replacing our own by a human federation of our single species throughout the globe—a very feasible project at the present day. If anyone objects that fighting is the only thing which prevents man degenerating, my reply is that there is still enough fighting to be done in connection with inanimate matter, animals, plants and microbes, to keep us from going to sleep on our peaceful laurels. Away with war—and may universal mutual service and syndiacony flourish among mankind!

Chapter IV

THE ANIMAL GUESTS OF ANTS (MYRMECOPHILES). MIMICRY

Forces which are eternally inexplicable to us, but which the metaphysicians, or self-styled philosophers, have called the *first causes of the Universe*, have never allowed one species out of all the living creatures known to make a collective mutual alliance or syndiacony with those of its own kind, or with other living creatures, unless this alliance is made at the expense of others. This rule is absolutely general—for every living thing grows, and in order to grow it must assimilate portions of other creatures, or at any rate, as in the case of plants, molecules which we call inanimate (for want of knowledge as to their intimate nature). In a word, every living thing must feed—even a world-federation of human races.

By *syndiacony* the Greeks meant the mutual help rendered by two deacons in the service of a third thief—man, as we see him, when we study ants, plants and human beings. This mutualism, therefore, must occur at the expense of a fourth, and that fourth, as we have seen, is represented by the other insects which ants destroy and consume in large quantities—to the advantage of our plants, which are devoured by these insects, and indirectly to the advantage of man, who cultivates the plants.

But if we extend the term syndiacony to the mutual alliance between ants and aphids, we are going beyond the Greek meaning of the term, for in this case the two deacons serve each other very well, but at the expense of plants and man. Nevertheless, we will retain the term, and the subject will be dealt with in Part III. Wasmann has used the term *trophobiosis*, which means 'nutritive life,' to denote the same principle. This is a pleonasm, for living and taking nutrition amount to the same thing, and I am not fond of pleonasms. The important point about the matter is *mutuality;* that is why I have adopted the term syndiacony, which implies services mutually rendered.

The present chapter will deal with the little animals which are fond of ants (myrmecophiles) and which consequently live near them, as guests, generally in their nests or at any rate in their immediate vicinity. But if they are fond of ants, that does not mean that they become useful to them—far from it! For the most part they are harmful. These little animals are legion. I. P. W. Müller in 1818, Savi in 1819, Märkel in 1841 and others since then, have drawn attention to the intimate relationships between ants and these little animals, but it is chiefly to the numerous works of the Jesuit Father Wasmann that we owe comprehensive studies in what may nowadays be called 'myrmecophily' (friendship with ants). The study of myrmecophily has become quite a special science. You may laugh at this, dear reader, but you will soon see how far the comprehensive study of a scientific speciality may lead us.

Wasmann was the master. Janet, Escherich, Wheeler, Reitter, Peringuey at the Cape of Good Hope, Kohl in the Congo, etc., followed him with such ardour that in 1910 we could already count 1,500 species of myrmecophiles, spread among 700 genera. Of these 1,500 species, about 1,000 were beetles; the rest were different insects of other orders, spiders, acari (mites), crustaceans, myriapods (millipedes), etc. But according to Wasmann and Escherich there must be more than 3,000 species of myrmecophiles altogether, nearly all of which show some degree of transition to parasitism.

Wasmann has divided the myrmecophiles into four groups which he claims are natural. In reality any attempt at classification here is artificial, and I will prove as much. Nevertheless, Wasmann's groups supply at least a basis. I should like to mention them here, and later on I will give typical examples of the first three, which are all that concern the present chapter.

1ST GROUP—SYMPHILY (friendship with). In true and complete symphily the guest is beloved by the ants, which regurgitate honey-dew to it and fondle it as an old maid pampers her spoilt little lap-dog. Furthermore, they rear and feed its progeny, from the larval stage to the chrysalis.

2ND GROUP—SYNŒKY (dwelling with). In a typical case of synœky the ant is *indifferent* to its guest. She seems to pay no attention to it, while the guest profits by her nest, where it dwells and acts as a scavenger, eating the refuse, the corpses and even certain parasites.

3RD GROUP—SYNECHTHRY (hostility towards). In typical synechtry the guest is abhorred by the ant. It hides in the nest or near by and attacks and eats the ants or their brood, only escaping their wrath by means of various tricks, which we shall consider.

Wasmann's 4TH GROUP is PARASITISM properly so called either *on* the bodies of ants (ECTOPARASITISM) or *in* their bodies (ENDOPARASITISM). We shall deal with this in Chapter V.

But before going any further, I should like to indicate here the *means* utilized by the myrmecophiles to achieve their aim. For the most part, these means are determined by hereditary instincts or by the structure of the body in each species—in other words, therefore, by phylogeny. As we said in Part I, and at the beginning of Chapter I above, this phylogenesis is by no means limited to natural selection; the engraphy (Semon) of characters acquired in the course of millions of generations plays a part in it which is at least equally important. This engraphy is borne as latent power by means of germs (eggs and spermatozoids) from generation to generation, adding every time a few latent atoms representing the individual's own acquisition. Thus in the infinity of time the hereditary mneme is gradually built up, and combined by means of natural selection. In accordance with the development of its brain, each little creature, whether ant or myrmecophile, adds to this instinct such small individual modifications or tricks as its memory allows. We have explained this before, and shall not deal with it again.

MIMICRY. Darwin explained by natural selection the striking imitation of the form, colour and movement of certain living creatures by others. Since his time, this phenomenon has been called *Mimicry*. Thus certain insects which live among leaves have the same green colour as they. Others can imitate a dry branch so closely as to be mistaken for it. Others again have the same colour, size, and form as insects which they hunt, or among which they live. By mimicry inoffensive flies have the deceptive appearance and even the special hum of bees, wasps or certain humble-bees whose sting they lack; and in this way they impose on their enemies the birds—even on men, and are a source of fear to them.

Mimicry plays an immense rôle in many ant-guests. In this matter, Wasmann has shown great perspicacity.

He has proved that the mimicry of the guests is adapted *to the quality of the ants' sensations.* In the guests of blind ants, colour as a rule *plays no part at all*, apart from cases in which these ants, such as *Anomma*, for example, come out into the open air from time to time and are followed by birds. In the case of ants with poor sight, colour-mimicry on the part of the guests is only a rudimentary affair, a rough approximation, but with regard to form, sculpture, hairs and smell, it becomes all the more striking—so as to deceive the touch and topochemical smell of ants. There is also a singular mimicry of demeanour, consisting in the activity of the limbs, in the mutual antennal language that passes between the guest and its ant, in caressing the legs, in its manner of eating and allowing or causing itself to be carried about, etc., and this kind of mimicry is not the least successful means of deceiving the ant's social instinct in a fashion that is as hypocritical as it is unconscious.

We must bear in mind, that among ourselves also the unconscious liar, the victim of hysteria, himself believes in the reality of the invented stories which his sick imagination drives him to tell us—as in the case of the late celebrity Thérèse Humbert, for example. That is why unconscious liars or pathological swindlers lead us astray a hundred times more effectively than the conscious liar, who is aware that he is lying and afraid of betraying himself, and whose physiognomy, voice and demeanour do, therefore, actually betray him. Since he believes in his fictions, the hysterical swindler, on the other hand, acts quite naturally; he enters into his part in good earnest, with all his heart, and all his artist's passion. Like a really good actor on his stage, he carries us with him, even to the verge of tears—just as the good symphile of our worthy ants leads them unconsciously by the nose, or rather by the antennæ.

It so happens that only two or three months ago one of these victims of hysteria (human, of course) named *S*, wrote me a most imposing letter, full of the noblest and loftiest sentiments, asking me only to send him in prison, where he was being detained, as he said, for political reasons, a few books which he might give his poor comrades to read, for the edification of their minds. I, though formerly in charge of an asylum, let myself as well as my wife be duped by him. He then begged me to intercede for him with the Minister of Justice in his country, which I did in all innocence. However, the Minister was good enough to open my eyes to the truth, concurrently with one of those same comrades the prisoner had mentioned, who had wind of the matter and was indignant about it. *S*. was a certified hysterical swindler. If he had not himself believed in his own lies, he would not have committed the blunder of referring me to the Minister of Justice, whom he knew to be rightly informed. You see, therefore, that the idea of mimicry is very complicated.

Mimicry is not only addressed to the various senses, sight, smell, etc., but appeals also to the mind and feelings, by means of movements and demeanour. If animals could write, they would be mutually deceived by letters, as men are. Our Plate IV shows in *a* and *b* a fine example of mimicry of form and colour as between a clear-sighted ant, *Sima rufonigra* of India, and a winged hymenopter which imitates it. Again, *c* and *d* show a bug, *Dulichius Wroughtoni*, which is a lifelike imitation of *Polyrhachis simplex* of India and Asia Minor; *P. simplex* also has good sight. In the same plate, *e*, *f*, *g* and *h* also show ants which imitate other ants, but that subject belongs to another chapter, and we shall deal with it in Part IV.

TRICHOMES. By trichomes we mean patches of a thick and more or less reddish-brown pubescence which covers certain parts of the body in the ant-guests, especially the symphiles. It can be seen on the abdomen, thorax, and elytra (hard wings) of beetles, and on the antennæ, etc. These trichomes give out an aromatic smell, which Wasmann describes as volatile, and which causes such delight to the ants that they may develop a passion for it—like the smoker's passion for tobacco, except that it is innate and instinctive. Later on we shall see the injurious results it has at times upon ants. Some trichomes are more upright and isolated than the rest, but all are hairs. Wasmann's microscopic examination has revealed the fact that every trichome is filled with fat-cells which secrete the volatile aroma so beloved of the ants. This accounts for the fact that they continually lick the trichomes of their symphiles.

POROUS CANALS. Other symphiles, however, are licked by ants without possessing trichomes. They simply secrete their aroma in certain porous canals in their chitin. These pores are analogous to those we learned to recognize in Part I, when dealing with anatomy. These insects have then a shiny and more or less oily appearance. Curiously enough, the converse also takes place: certain symphiles lick the bodies of their ants instead of being licked by them. In this case it is the ant in whose chitin certain porous canals secrete a fat or aromatic oil.

OFFENSIVE OR AGGRESSIVE MEASURES. These are adopted by the Synecthrans, and sometimes also by the Synœketes, and they are of many kinds.

A thick hard carapace, combined with a stumpy figure, hidden or enlarged antennæ and short, retractile legs, renders certain synechthrans, such as the Histerid beetles, almost invulnerable, and enables them to brave the ants and devour their brood. Another device of the aggressor is a convex disc which hides the legs and antennæ when they are folded under it. Some discharge disagreeable smells at the ants when they are attacked, and so repulse or stupefy them. Others again escape them by the extreme rapidity and skill of their movements, whereas in many cases some ruse is efficacious.

Certain *Paussus*, which are more in the nature of symphiles, as well as the little *Brachinus crepitans* or bombardier beetle, produce petards which they throw noisily, not against the ants their hosts, but against the 'common enemy.'

INTERNATIONAL RELATIONSHIPS. By this somewhat singular term Wasmann means the friendly relations between guests, particularly symphiles, and various colonies, either of the same species or of different species. The synechthrans are everywhere the enemies of the ants, and hence they are excluded from all international affairs at the very beginning of things. The indifference of the ants to most of the synœketes, on the other hand, in itself renders them practically international, except when they bear with them an 'enemy odour' that is too pronounced. But its distinctly friendly relations render the symphile so dependent upon its ant or ants that it would change from one formicary to the other at grave risk to its life if the attraction of its trichomes did not usually outweigh the ant's hatred of an 'enemy odour.' Nevertheless, a struggle between attraction and disgust often takes place in the ant: it is this struggle—generally a short one—between two instinctive sensations and feelings which Wasmann calls 'putting a guest in quarantine.' But there are certain cases in which the friendly symphile instinct is so far fixed by heredity between one species of ant and the guest specially adapted to it, that each colony, hostile to the other colonies of this same ant, immediately adopts the guest in question without any quarantine.

There are a thousand shades of difference between these cases, but as a rule a quarantine of about an hour is enough. During this quarantine, the ants give unmistakable signs of doubt and mistrust; they threaten or pester the guest to a greater or less extent. On her side, the guest does all she can to calm the ants by caresses in the antennal language; but it is chiefly the alluring odour of the trichomes which rapidly disarms the fears of the entire colony, and hastens the friendly adoption of the symphile.

Such are the means which the myrmecophiles employ to exploit the collective instinct of their hosts. We will now consider some typical cases.

SYMPHILES

I will take as a type the genus *Atemeles* (*paradoxus pubicollis*, *emarginatus*, etc.). In Fig. 32, I introduce you to an *Atemeles*, which is soliciting honey-dew. It is caressing on both sides the head of its host, a worthy and hard-working European *Myrmica*, whose temper for that matter, is none too sweet, and which has a powerful sting. It is also tapping her amicably with its two antennæ! We may be puzzled as to why the *Myrmica* should thus allow herself to be duped by this hypocritical and treacherous parasite; for not content with actually dragging the product of her labour out of her, the creature has from its infancy, the carnivorous larvæ stage, devoured the brood of the ant, which will nevertheless feed it in a most maternal fashion. But the answer to the problem lies in *Tr.* in this figure,

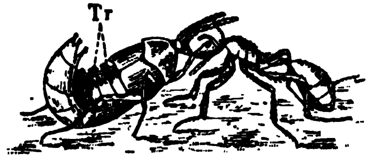


Fig. 32

for the quarantine is over and the lure of the trichomes with their seductive odour has conquered the initial fears of the *Myrmica;* she is disgorging from a full crop into the mouth of the intruder the food which an ant's social duty requires her to give to her own larvæ.

In this we behold the momentary craving for pleasure which drives a man, unconsciously, in the toils of an hereditary instinct, to go and get drunk with alcoholic liquor which causes direct degeneration in his progeny, just as the trichomes of the *Atemeles* causes indirect degeneration in that of the ants; and furthermore makes him a lunatic and a criminal, which the trichomes do not do. The analogy is stronger than one would suppose. Men are really lying to themselves when they pretend that only the abuse of alcohol is harmful. They all imagine that they can remain moderate drinkers, whereas, quietly and imperceptibly, most of them fall into an abuse which may be temporary or may be enduring. And on this abuse our parasites live—the publicans and alcohol merchants. By way of trichomes they have the butlers, and more particularly the lying press, which they subsidize. Finally, what is more, the infection may become collective or national, as in the ant-colonies. Then we shall see the countries most infected, like France and Latin Switzerland of the present day, producing foolish advertisements of their 'vintage of Bordeaux or Yvorne,' with which they try to infect Norway, Iceland, or their compatriots, pretending that wine is not alcohol, that it has strengthening power, that abstainers are wicked fanatics, that the prohibition of alcoholic liquor in the United States is a failure, and other similar lies, designed to exploit their fellows shamelessly as individuals and communities, for monetary gain. We must admit that beside facts like these the seductive trichomes of the *Atemeles*, which have no press at their service, are rather of the nature of an anodyne.

We will now study our little friends at somewhat closer quarters, as Wasmann did. After hibernating with a worthy *Myrmica*, dwelling in its nest and being fed by it, in the manner we have just described, our *Atemeles* has only to regale her, that is, intoxicate her with its aromatic trichomes, which the ants are for ever licking. But in the following spring it abandons its nurse-mother and, after mating with a supernumerary, emigrates to the home of another ant, such as *Formica fusca*, *rufa*, *pratensis*, and for good reasons. Its instinct drives it to an ant that is better adapted than *Myrmica* to bring up its larvæ. It therefore enters a *Formica* nest, where after a short quarantine it obtains adoption and regurgitation. The female then sets to work to lay her eggs, or rather her larvæ, on a heap of eggs, belonging to the *F. fusca*, let us say. Wasmann has proved that most *Atemeles*, like the *Lomechusa*, are viviparous—that is, the eggs are already hatched in the body of the mother, who then lays the larvæ directly.

These larvæ waste no time, and, like the vermin they are, they immediately set to work to devour the eggs of the *F. fusca*; then, when they have grown bigger, they also devour the larvæ and nymphs. Thus we may watch the *Formica* brood diminishing in proportion to the number of *Atemeles* it contains. And the good *F. fusca* continue, none the less, to care for those wretched cuckoos as the apple of their eye, and even to disgorge honey-dew to them just as they do to their own larvæ, for the *Atemeles* larva loves change in diet, honey after meat, or *vice versa*.

It was I who first discovered the *Atemeles* larvæ, between the years 1869 and 1873, without knowing as yet to what insect they belonged. I saw them in various formicaries where the *Formica* were regurgitating honey-dew to them, carrying them like their own brood when they were fleeing after a defeat, in short, taking as much care of them as of their own larvæ. But most amusing of all was the following fact: the slave-making species *Polyergus rufescens*, or Huber's Amazon ant, go on warlike raids in which they plunder the larvæ and nymphs of *Formica fusca* and *rufibarbis* in order to hatch from them auxiliaries which are just as unconscious of their slavery as the larvæ of *Atemeles* are unconscious of their crimes. And I have on many occasions watched raids in which the Amazon ants carried off as booty a large number of *Atemeles* larvæ. Without suspecting what she was doing, the thief was carrying off another robber, which was almost certain to pay her back in ample measure by devouring her larvæ and slyly appropriating from her slaves the honey-dew for which it too had such a craving: you will admit, dear reader, that this affair is not without its piquancy.

On reaching maturity, the *Atemeles* larva collects earth all around her and enshrines herself in a cocoon on her own account, with a view to becoming a nymph. The ants often help her do this, and here a curious phenomenon is brought about. If she is to make a success of things, this nymph must remain in the earth until hatching-time. But since instinct urges them to unearth and clean their own cocoons, the ants often act in the same way towards the *Atemeles* nymphs, to which such a proceeding is disastrous. Accordingly they dry up and perish, or else they are devoured by the ants, which thus pay them back tardily 'an eye for an eye.' If she is to emerge alive at the appointed time, the *Atemeles* nymph must be 'forgotten' or 'neglected' by the ants and come out alone from the cocoon, which remains in the earth. And Wasmann has shown that as a colony of *F. fusca* or *pratensis* becomes more and more degenerate and full of pseudogynes, in consequence of the infection received from *Atemeles*, it tends more and more to forget and neglect the cocoons buried by the *Atemeles*, and to desist from unearthing them. And in this way the evil and the degeneracy grow worse instead of better.

From birth to the adult state, the ontogeny of an *Atemeles* lasts about two months. *A. emarginatus* is ovo-viviparous, that is, it lays eggs which become larvæ directly afterwards. When successfully hatched, generally in the month of August, *Atemeles* steals away without so much as a word of thanks to the *Formica* which have nursed her at their own expense. It then goes and hibernates once more with a *Myrmica*, and so on, year after year!

It is a well-known fact that as a colony becomes more and more infected by *Atemeles* (or *Lomechusa*) we find in its midst more and more of those curious hunch-backed ants called *pseudogynes*, which are represented in Fig. 33. I have attentively studied the behaviour and habits of these degenerate creatures, whose origin was as yet unknown to me in 1874 when I wrote my book *Les Fourmis de la Suisse*. Without any pre-existing bias, therefore, and taking them at the time for simple intermediate forms between the ♀, whose humped thorax they possess, and the worker which is wingless like them, I made the following statement: The pseudogynes work in the formicary like simple ☿, but *to a much less extent.* They are also less

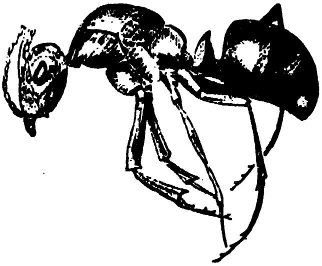


Fig. 33

intelligent; their brains are smaller. They are not fertile and are often almost smaller than the smallest ☿. I remember observing for a long time, near Munich, a *F. rufa* nest swarming with *Atemeles*, in which the pseudogynes, which were often extraordinarily small, constituted perhaps a third of the worker population.

Wasmann has proved conclusively that the presence of *Atemeles* (and of *Lomechusa*) always and everywhere coincides with that of the pseudogynes.

Viehmeyer, however, made the following decisive experiment: from a colony which some *Lomechusa* had for years been filling with pseudogynes he removed an old *sanguinea* queen which had been producing these degenerate creatures and caused her to be adopted by the ☿ of a colony which was absolutely healthy and free of these odious guests. Henceforth, this same old female ceased altogether to produce pseudogynes; her eggs no longer gave rise to any but wholly normal ☿. The trouble in question therefore cannot be the equivalent of what I have called in man blastophthory or germ-deterioration, by means of alcohol, for instance. The degeneracy of the pseudogynes remains none the less real, like their intimate connection with the presence of *Lomechusa*, *Atemeles* and *Xenodusa*. But the relationship of cause and effect is still unknown to us: it demands new and *precise* investigation. Research of this kind is reserved for the future. In the meantime we must be content to set down facts; and I can only say that my own observations everywhere, and those of my colleagues, confirm Wasmann's theory: *Atemeles* and *Lomechusa*, cause; pseudogynes, effect.

The *Atemeles* have their special ants: *A. emarginatus* passes regularly from *Myrmica rubra* to *Formica fusca*, *A. paradoxus* from *M. rubra* to *F. rufibarbis*, and *A. pubicollis* from *Myrmica rubra* to *F. fusca*—in every case from a *Myrmica* to a *Formica.* But by means of patient experiments Wasmann has succeeded in making *Myrmica rubida* and even *Aphænogaster* and *Stenamma* receive the *Atemeles*, owing to the caressing and persevering wiles of the symphiles, but not without a long and violent quarantine.

We may add that *Atemeles* exudes a strong smell analogous to that of *Tapinoma;* this I stated as early as 1874 in my *Fourmis de la Suisse.*

SYNŒKETES

I will here introduce as a typical example, a little Staphylinid beetle 3 or 4 millimetres long, named *Dinarda dentata.* It lives as an indifferently-tolerated guest with *Formica sanguinea* (rarely with *F. fusca*) and its slightly larger colleague, *Dinarda Märkeli*, which is 4 or 5 millimetres long, is a guest of *F. rufa* and *pratensis.*

D. dentata is depicted in fig. 34 at the height of its activity, engaged in ridding a *Lomechusa* much larger than itself of the mites which beset her, and eating them.

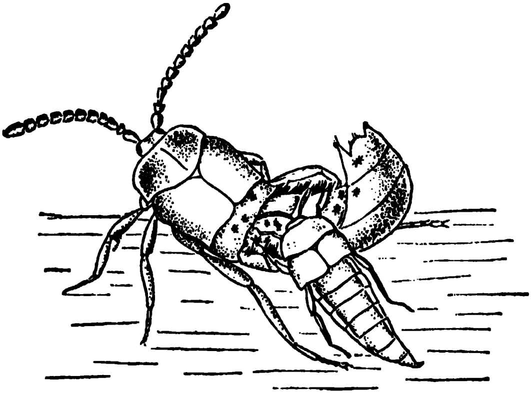


Fig. 34

The *Dinarda* are certainly very useful to their ants, and act as their nest-scavengers. They feed on the corpses of ants and nymphs, on all the useless refuse which is in danger of going mouldy, on mites which suck and torment the ants, etc. It is very uncommon for a *Dinarda* larva to eat an ant-egg. The *Dinarda* have the colour of their ant, but they are neither fed nor licked nor reared by her, because they have no seductive trichomes. They are honest little animals, which do not fool those that shelter them. This is probably the reason why the ants regard them with indifference and contempt, even with suspicion—for the world *wishes* to be deceived and flattered; honest folk are mistrusted and laughed at, among the ants as among ourselves.

The *Dinarda* mate in March, and their little larvæ, which are as agile as they are portable, are born in April; during May and June they are growing. They feed like their parents, and dispute with them the waste-products of the ant-nest. Sometimes, so Wasmann tells us, a big larva will eat a smaller one or even an ant-egg, but they are so entirely independent of their hosts that the adult *Dinarda* and the ants disgorge nothing whatever to them. On reaching maturity, they enter the earth to achieve their transformation into nymphs; they come out as perfect insects, and keep out of the way until their chitin hardens. The *Dinarda* have two generations per year, and according to Wasmann, they live for only six to nine months.

That the ants manifest sheer indifference to the *Dinarda* is due, not only to a certain instinctive adaptation, but also to a habit individually acquired. The *Dinarda* are in fact *unassailable*. The whole structure of their body and the suppleness of their movements appear specially *calculated* to render them invulnerable to the attacks of the big ants.

Their broad, flat thorax is adapted to the ground, their elytra are hard and angular; the abdomen ends in a hairy point, from which the ants slip every time they try to bite; the antennæ and legs are short, and fold back easily under the flat body; finally, the skill of the little beetle, in twisting its tail and getting out of the way, render it almost impossible, as Wasmann says, for a *F. sanguinea* or *rufa* to do any kind of harm to a *Dinarda* which is sound and sufficiently hardened. Wasmann once saw a *F. sanguinea* in an excited mood setting upon a *Dinarda* which was exhausted after mating, and attacking it in vain with its mandibles for a quarter of an hour. Since it could not escape, the *Dinarda* contented itself with folding its legs and antennæ, and thus emerged unscathed from the conflict. Here the relative smallness of the *Dinarda* is a help to them; the small ants are more dangerous to them because they are better able to catch hold of the beetle's extremities.

The international relations of the *Dinarda* are usually limited to the various formicaries of the species which lodges them, for they have no winter station distinct from that of the summer, as the *Atemeles* have. While dwelling in the nest of their *Formica*, they mix with her less intimately than the *Atemeles*, and, unlike the latter, they do not gather into one confused mass with her or her brood. For the rest, signs of defiance on the part of the ant are somewhat exceptional; otherwise, *F. sanguinea* would not allow her *Dinarda* or *Lomechusa* to despoil her of her mites, as they both do, in such a serene and kindly fashion.

SYNECHTHRANS

I will here take as my example *Myrmedonia funesta*, which is adapted in size and colour to *Dendrolasius fuliginosus*. In appearance it is somewhat similar to the *Atemeles* and *Dinarda*, so we need no illustration. This creature is frankly a robber—quite as frankly in its way as the *Dinarda* in theirs; and robbers of its kind are hated and persecuted by the ants. They do not live inside the nests, but simply keep watch over the ants at the entrance of their dwelling or in its immediate vicinity; or sometimes they hide in a corner behind an earthen rampart, and may frequently be protected by a deceptive mimicry of colour and form.

Myrmedonia funesta will lie in wait to surprise an isolated *Dendrolasius fuliginosus.* Wasmann has watched five or six of them thus attack a *Dendrolasius*, and then quarrel among themselves over her flesh, when they were tearing it to pieces. When an ant attacks a *Myrmedonia*, it discharges a nauseating secretion at her head, and forces her to draw back. The *Myrmedonia* usually emerge and attack during the night, or when the temperature falls. *M. humeralis*, which attacks *Formica rufa*, is of the same red colour as she.

Between the *synechthri* and their ants there is thus perpetual guerilla warfare. These skirmishers are the exact opposite of the symphiles in the matter of love, though, like them, they do grave harm to the ants! But a frank enemy is better than a hypocritical friend, which not only exploits them but produces trichomes and pseudogynes!

SPECIAL CASES

As Wheeler has very aptly said, the myrmecophilous ant-guests are an inextricable medley of scavengers, satellites, exploiters, commensals, assassins, and parasites. Instead of continuing to classify them, therefore, we will simply enumerate the various principal kinds of creatures which enter into this medley, and the combinations of their habits.

LOMECHUSA AND XENODUSA

Lomechusa strumosa is represented in fig. 35 *A* and its larva in fig. 35 *B.* These beetles and their kindred have

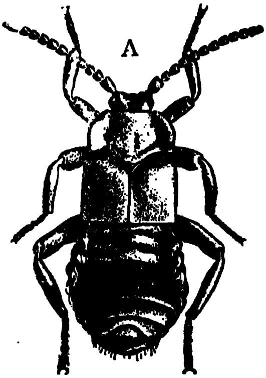


Fig. 35 *A*

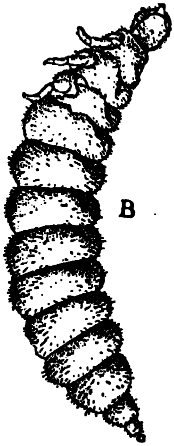


Fig. 35 *B*

habits very similar to those of the *Atemeles*, and are all guests of *Formica sanguinea*, with the exception of *L. inflata* of Lapland, which is the guest of *F. rufa*. It matters little whether this *F. sanguinea* has slaves or not, for *Lomechusa* is present as frequently in the one case as in the other. On the other hand, it is very seldom that we find it in the autonomous ant-colonies of the slave-species *F. fusca* or *rufibarbis*. The *Lomechusa* are somewhat heavy and clumsy. The ants cram them with food as they do their larvæ, and not as they do in the case of their companions or the *Atemeles*.

This is how it is done : The *Lomechusa* taps the ant lightly with its antennæ and licks its mouth. If she is inclined to regurgitate, the ant allows the beetle to place its little head in her mouth. After this *Lomechusa* remains almost completely quiet while the ant slowly disgorges the dainty, moving her head to right and to left. When this is over, the two insects generally lick each other's mouths. A feeding process such as this lasts from twenty seconds to four minutes, according to circumstances. *Lomechusa* never caresses the sides of its ant's head as *Atemeles* does; it is passive, while *F. sanguinea* is active; herein it is unlike *Atemeles* or any ant which is begging a companion for regurgitation. An exception once observed by Wasmann only confirms the rule.

The *Lomechusa* pass all their lives in the home of the *F. sanguinea;* they have no summer and winter quarters, like *Atemeles.* This stability provides the key to a great many of their habits. Their larvæ are fed and nursed by *F. sanguinea* and her slaves, which does not prevent them from devouring the ant-eggs. Wasmann has made the following very interesting experiments on the way in which the *Lomechusa* are received by strange colonies, either of *F. sanguinea* or of other species.

a Lomechusa taken from sanguinea colonies which already possessed them and placed in other sanguinea colonies which also possessed them. Here the general rule is the immediate acceptance without quarantine and without the ant's making any distinction between the new guests and their predecessors. On April 30th, for example, six *Lomechusa* were taken from three different colonies and put into a fourth. After a short and friendly stroking with the antennæ, or even without it, all the *Lomechusa* were immediately admitted on the same footing as the old guests; it was the same in other cases.

Once, however, when Wasmann put a *Lomechusa* from another colony possessing the same guest into a *sanguinea* colony, which already harboured a *L. strumosa*, the ants and their slaves came forward for a few seconds with their mandibles half-open and with enquiring antennal motions. The beetle then moved its antennæ and raised its abdomen very high. The pacified ants at once walked away and joined in the teeming throng of their companions. Five minutes after, a *sanguinea* licked long and gently the trichomes of the *Lomechusa*, which mated half an hour later with one of the old *Formica* guests, right in the midst of the ants.

b Lomechusa put in sanguinea colonies which had formerly possessed none. Here, too, admission was generally immediate. In a district where Wasmann had never found a single *Lomechusa* within a mile's radius, he placed two ☿ *sanguinea* of a large size in a glass with a *L. strumosa;* the latter was not attacked. The next day he added a large number of ants. Some of them opened their mandibles with a menacing air, or even tried to seize hold of the beetle's abdomen. The beetle at once began to tremble all over its body and to wave its antennæ briskly about. When Wasmann added still more *sanguinea*, a general tumult ensued and the *Lomechusa* became greatly agitated. It began to dance in a ring, in a fashion as comical as it was clumsy, and tried to strike with its antennæ, which were in a perpetual state of oscillation, every ant that came near it, even if she were paying no attention to it. In spite of the general unrest, none of the ants troubled the beetle any further. When peace was to some extent restored, Wasmann gave the ants a piece of sugar. A moment after, he saw a *sanguinea* disgorge a drop of honey-dew to another, raising the front part of her body and ejecting a large drop on to the out-thrust lower lip of her companion. Then up came the *Lomechusa* and raised the front part of its body in the same way, trying as it did so to reach with its head the mouths of the two ants, and licking their heads and antennæ. And last, when the *sanguinea* which had received the drop and been satisfied drew her head away, the beetle took her place, striking with its antennæ the head of the regurgitating ant, which it tried to lick. After a few seconds, this ant allowed the *Lomechusa* to place its head in her mouth and thus to lick up the precious liquid. This was the only time that Wasmann saw a *sanguinea* disgorge to a *L. strumosa* in the manner which ants employ for each other, not for their larvæ.

But in a large number of other experiments, even those made upon specially irritable colonies, in which the *sanguinea* did not as yet know the *Lomechusa*, and would attack *Dinarda*, for instance, the *L. strumosa* were always rapidly and amicably adopted, without any quarantine or sign of suspicion. It was quite otherwise, however, with *Atemeles*. Even in colonies containing *Atemeles*, the *Lomechusa* were at once admitted, *whereas every newly-presented Atemeles had to submit to a lengthy process of quarantine or be torn to pieces by the ants*. Here again, we see the fallacy of great generalized dogmas. Here we have two little creatures, very near of kin and both guests of the same ant-species, both furnished with alluring trichomes and both received under the same conditions. Why should the one have to endure pitiless quarantine under pain of being torn to pieces, despite all its tender caresses, while the other is promptly and kindly received ? We must learn to ask the question without seeking hypotheses in answer to this 'why,' until some new fact comes along and explains it to us.

Wasmann formed by artificial means, as I had done before him, some little 'autodidact' *sanguinea* colonies, that is, colonies consisting exclusively of nymphs hatched alone. Once again—the *Lomechusa* which he gave to these colonies were also speedily and kindly admitted; their larvæ were also fed by the ants. Here we have irrefutable proof that the adoption of this guest, at any rate, and its larvæ takes place by hereditary instinct, though the influence of the trichomes is, of course, not thereby excluded.

c How do the fusca and rufibarbis slaves or auxiliaries of F. sanguinea behave towards the Lomechusa ? Generally speaking they treat them kindly when they have once been admitted by the *sanguinea*, but they lick their trichomes much more often than they regurgitate honey-dew to them.

After the admission of new *Lomechusa*, it is the *sanguinea* alone which play an active rôle ; the auxiliaries usually appear indifferent. They scarcely ever display any sign of mistrust, but they can only accustom themselves slowly to friendly relations with the beetle. Nevertheless, in all formicaries which were very rich in auxiliaries, Wasmann sometimes saw these auxiliaries open their mandibles for a moment and betray their suspicions of the intruder. The *Lomechusa* are only under exceptional circumstances the guests of natural *fusca* and *rufibarbis* colonies. Wasmann explains the indifferent or friendly way in which the auxiliaries at once received these guests by the fact that, when the *sanguinea* also promptly lick their bodies, they communicate to them the *odour* of the nest and the formicary. He cites a case which speaks strongly in favour of this view.

d Relations between Lomechusa and F. rufa and pratensis

L. inflata of Lapland seems to be a regular guest of *F. rufa*. According to Tickler, Sahlberg, etc., our *L. strumosa* is sometimes found in her colonies, though Wasmann had never been able to discover it there. But for good reasons he regards *L. strumosa* as a *secondary guest* of *F. rufa* and *pratensis*.

The results of numerous experiments certainly prove that after making a short examination, with their mandibles open, or even immediately, without examination or quarantine, *F. rufa* and *pratensis* adopt the *L. strumosa*, lick its trichomes and feed it. It makes an agreeable impression on their senses.

After a battle between *F. rufa* and *sanguinea*, Wasmann watched a *Lomechusa* belonging to the *sanguinea* on the field of the violent combat, in which the adversaries reciprocally drenched one another with poison, and saw her pass from the *sanguinea* to the *rufa*, and even go to their larvæ and move about among them as if she belonged there, without showing any anxiety. When a *rufa* examined her she waved her antennæ and all was explained, even if the *rufa* did open her mandibles for a moment. But as a general rule, although they are soon adopted by *F. rufa* and *pratensis*, *L. strumosa* seem to be less at its ease with them, less at home than with *F. sanguinea*. Wasmann once cut off the antennæ of a *L. strumosa*. Being thus unable to mollify the *F. rufa* with its antennæ, it was less well received. They took hold of it by the head, then by one leg, and then bit its carapace; all the ants opened their mandibles, while another *L. strumosa*, which had its two antennæ, was speedily and kindly received. Nevertheless, next day the two *Lomechusa*, the one without its antenæ as well as the other, were adopted on a footing of equality by the *F. rufa*. Here, again, we can see how various factors combine—in this case, the activity of the antennæ and trichomes—to expedite or delay adoption. The more we observe, the more the different causes and their varied and variable effects are multiplied.

e Relations between L. strumosa and F. exsecta.—This is a *Formica* with which this guest is not found under natural circumstances. When Wasmann put one in her nest, it was ill received at first, the *exsecta* threatening it with open mandibles and trying to bite it. But the *Lomechusa* was able to appease them by tapping them with its antennæ, and they licked it from time to time. Yet the *L. strumosa* did not feel at its ease with the *exsecta*, which treated it with toleration rather than friendliness. They licked its trichomes well, but gave the impression that they were playing with their guest, especially with its antennæ, which they often grasped by the base. Wasmann never saw them feed the *L. strumosa.* On the contrary, *Emphylus glaber*, another little beetle which Wasmann placed among the *exsecta*, and which is also a guest of *F. rufa*, continually used *L. strumosa* as a riding horse. It stood up on the creature's back for hours, and seemed to lick its trichomes. In spite of all, the *L. strumosa* remained for several weeks with *F. exsecta* without becoming any thinner. Hence it must have been able to feed itself. But the *Atemeles*, being more active and adroit than the *L. strumosa*, were better able to draw the attention and interest of the *exsecta* to themselves.

f Relations between L. strumosa and the ordinary F. fusca colonies. In June, Wasmann put among some *F. fusca* a *L. strumosa* which had already lived with *F. sanguinea*, *rufibarbis*, etc. The *F. fusca* attacked it violently, biting it and seizing its antennæ. The *Lomechusa* defended itself by odoriferous discharges, holding its abdomen very high, and this only irritated the ants still further. After a few moments, however, the attack ceased and the beetle gradually grew calm; a *fusca* continued to pluck at the hair of its abdomen, but in between whiles she began to lick it. Another began a gentle and persistent licking; in her case, greed seems to have triumphed over anger. Five minutes afterwards, the *Lomechusa* was peacefully surrounded by numerous *fusca*, which were licking it. An hour later a *fusca* was already feeding it, larva-fashion, licking its mouth and head during the intervals. For five minutes she continued this system of alternate feeding and self-indulgent licking. The next day no more attacks took place, but the *fusca* paid less attention to the *L. strumosa* than they had done the day before, when the novel event had occurred: they contented themselves with licking it from time to time or plucking its hair. In a second and entirely analogous case, a *L. strumosa* was adopted after a quarantine consisting of a quarter of an hour's hostility and an hour of alternate peace and quarrelling. The insatiable greed of *F. fusca* can also be seen in connection with *Atemeles*, whose trichomes they lick with such fierceness as to wound the beetle. The ant then sometimes ends by devouring it. The larger *Lomechusa* can defend itself somewhat better.

g Relations between L. strumosa and the ordinary rufibarbis colonies. Here the quarantine begins with a violent attack on the part of the *rufibarbis*, which bite the *Lomechusa* and even drench it with poison. But the *L. strumosa* replies by repeated odoriferous salutations, which scare the *rufibarbis* and make them desist. A friendly licking process then begins, and in an hour's time the beetle is adopted and even fed. *Rufibarbis* has a sanguine temperament, quickly aroused to anger, but also quickly reconciled.

Incidentally, according to Wasmann, *L. strumosa* is much more easily adopted—almost immediately, without serious quarantine—by colonies of Amazon ants (*P. rufescens*) than by the ordinary colonies of *F. fusca* and *rufibarbis.* The amazons ignore the beetle and the slaves welcome it.

h Relations between L. strumosa and Myrmica (Neomyrma) rubida. The large *M. rubida* gives a most painful sting, but her temperament is calm and not very aggressive. A *L. strumosa* which Wasmann put among them on September 4th was first seized by several ☿ and even threatened with their stings. On one occasion, indeed, it was slightly stung. But between five and fifteen minutes later it seemed to have been adopted into the midst of the ants, which were licking its trichomes. When Wasmann cut the antennæ of a second *Lomechusa*, he saw it violently attacked, bitten and stung, so that it was afterwards lame and paralysed, as though drunk, since it had been unable to appease the *Myrmica* with its antennæ. A third *L. strumosa*, which had not been amputated, was welcomed like the first, but stung on one leg. Rearing itself up, it then emitted a volley of odour which only irritated the *Myrmica*. By evening, all three *L. strumosa* were trembling, and the second one without antennæ was dying and still being attacked; the other two were limping, but their hosts enjoyed licking them for a long time. Next day the second was dead, and the first fairly well recovered. Wasmann then put into the nest a fourth *Lomechusa* with its antennæ cut off. It was threatened by the mandibles of its hosts, but not stung, and was adopted within five minutes. It therefore seems as though *M. rubida* grows accustomed to *L. strumosa*. Actually, a fifth and a sixth *Lomechusa* were received during the two days which followed, and adopted almost immediately, after scarcely any threats, by the *M. rubida*. They were amicably licked, but not fed, and lived in this manner with their hosts during the days that followed.

On September 12th, Wasmann placed some *Atemeles paradoxus* and *emarginatus* in the same *M. rubida* formicary. But here the habit they had acquired with *Lomechusa* had no effect: the first *Atemeles* were stung and died; the others, however, were adopted just like the *L. strumosa*, and, what is more, by means of their persevering caresses, which were more artful than those of *Lomechusa*, they presently coaxed the *M. rubida* to feed them.

i Relations of L. strumosa with Lasius umbratus and Dendrolasius fuliginosus. The first took no notice of the *Lomechusa*; no adoption took place. On the contrary, the *fuliginosus* bit it and covered it with poison, licking its trichomes, however, between whiles; but they did not appear to adopt it definitely. The *Lomechusa* remained in a corner, ill at ease; the odour as well as the suspicious and continued indifference of *Dendrolasius* evidently did not please it! When he rubbed a

L. strumosa with a mutilated *D. fuliginosus* in order to communicate her odour to it, and then put it back among the *F. sanguinea*, Wasmann found that it was first received with open mandibles, then stroked with their antennæ, but always recognized as a friend, and caressed. But when he rubbed a ☿ *sanguinea* in the same manner, she was still less well received by her companions than the *L. strumosa*, and even drenched with poison and pulled roughly about before she was recognized. The effect of a deceptive enemy odour is here as clear as daylight.

k Relations between L. strumosa and Lasius flavus. Here there was no adoption; but the peaceable and frail *L. flavus* feared the intruder, and seeing that it was not enough to take hold of the creature by the legs, they did the same with it as with other dreaded intruders. Profiting by their skill as masons, all the ☿ brought pellets of damp earth to the spot, and soon the poor *Lomechusa* was buried alive.

l Relations between L. strumosa and Camponotus, Myrmica rubra, Lasius niger, Tapinoma erraticum, Tetramorium caespitum and Leptothorax. All these ants simply killed the *Lomechusa* and did not adopt them, except for the peaceable *Leptothorax*, which avoided them. The *Camponotus ligniperdus* bit or decapitated them, though they licked them a little from time to time.

The above long list is very instructive by reason of the insensible transitions between instincts and acquired habits with which it presents us. We are greatly indebted to Wasmann on this account.

m Relations between Xenodusa and ants. All the species of *Xenodusa*, which is very similar in appearance to *Lomechusa*, live in the United States, as the guests of various species of *Camponotus*. I myself have found *X. cava* living with *C. pennsylvanicus* in Connecticut, inside a rotten tree trunk inhabited by these ants. But Wheeler has proved that they are alternately, like *Atemeles*, the guests of two ants. They hibernate with *Camponotus* and emigrate in the spring to the home of a *Formica* which rears and also feeds their larvæ. Like *Atemeles*, they know the art of caressing with their fore-legs the ant which feeds them. This ant also produces pseudogynes, as Wheeler has proved in the case of *Formica incerta*.

THORICTUS

As early as 1889, I discovered at Gabès, in Tunis, a little beetle which was always attached to the antennal scape of the large, long-legged *Cataglyphis bicolor*, an inhabitant of the oases. It is found inside the nest as well as outside. I sent it to Wasmann, who afterwards named it *Thorictus pauciseta*. It represented a new species, and bore trichomes. Wasmann and I thought that it must have been attached to the ant's scape for the sake of being carried about when the ant moves its quarters. Other guests travel on their own legs, but those of *Thorictus* are too short, and *Cataglyphis* marches so quickly that it would be impossible for this tiny guest to follow along the sand. There can be no doubt that *Thorictus* is thus carried during the removals of *Cataglyphis*. I have pointed this out in the German journal *Humboldt* (Vol. IX, No. 9, 1890).

In March, 1893, I landed at Oran in Algeria. While waiting for the train to start, I dug out a *Cataglyphis megalocola* nest with my chisel, and was surprised to see inside it some ☿ carrying little beetles attached to the scapes of their antennæ. There were several of them. When poured into a tube of alcohol they separated from one another. I put several specimens of these couples into a closed box, detaching the beetles from the ants' scapes myself. As soon as I arrived at the town of Perrégaux, where my brother-in-law, Édouard Bugnion, was waiting for me, I mentioned my discovery to him. He lent me a flask of cyanide of potassium, and I was then able thereafter to kill the *Cataglyphis* and their guests so instantaneously that the latter remained attached to the scapes in death. At Perrégaux, we found numbers of these interesting beetles, and always in the company of the same ant; it was a new *Thorictus* that Wasmann named *T. Foreli.* Next morning I opened my box again; the *Thorictus* detached by me the day before had all climbed back on to the scapes of their ants.

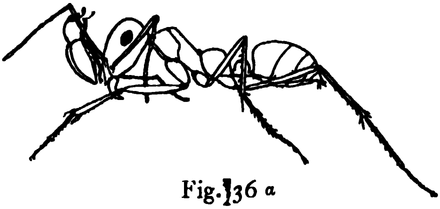


Fig. 36 α

In fig. 36, dear reader, I present to you my *Thorictus.* In α you see it as I have drawn it myself, mounted on the scape of its ant, and in γ the same in front view. It is just one-third as large as the head of *Cataglyphis*, which sometimes carries one on each of its two scapes. In β, *E* shows you the little beetle's prothorax, enlarged, *D* the head and antennæ, *C* the mandibles and *A* the epistoma deeply and precisely hollowed out in a bold semi-circle. *B* denotes the ant's scape, enclosed no less precisely between the epistomary groove and the mandibles of the *Thorictus*—a splendid adaptation of form to instinct! There are several other species of *Thorictus* living among the ants, which do not, however, fasten themselves to the scape. They have a

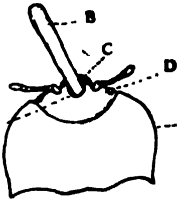


Fig. 36 β


Fig. 36 γ

hollow on the front edge of the epistoma, but it is much broader and rounder, and could not encircle a scape like that of *T. pauciseta* and *Foreli.* The transitions of habits and forms, in this case, have still to be studied.

In Algeria I found *Thorictus Foreli* again, though more rarely, in the company of *Cataglyphis mauritanicus*, and at El Kantara, Biskra, etc., I very often found *T. pauciseta* with *C. bicolor.* I noticed that the ☿ which carry it have a lazy or weary air. On the other hand, I have not observed the desperate and vain efforts which they make, according to Escherich, to rid themselves of this inconvenient guest by using their legs, putting their antennæ into crevices, or maybe striking their scapes against the walls of the nest. It is true that my observations were made during a journey, and could not have been other than superficial.

But that is not all. Wasmann observed that the scapes of the *Cataglyphis*, encircled by the *Thorictus*, possess little canals or enlarged pores, sometimes covered with a drop of dried blood. He concluded from his examinations, made with a lens, that *Thorictus* sucks the blood of its ant through the scape, like a little vampire. This view, as to which I was at first very sceptical, is strongly supported by the mouth-structures of *T. Foreli*, compared with that of another species which lives with *Messor.* This creature does not encircle the ant's scape, and its mouth, under normal conditions, is ordinary. The sharp point of the jaws in *Foreli* is twice as long, and entirely covers the lower lip, as well as the labial palpi. The lower lip itself is somewhat reduced, if not exactly atrophied, as well as the short, thin labial palpi. Wasmann thinks that *Thorictus* uses the long point of its jaws to pierce or enlarge a porous canal in the chitin of its ant's scape, and then sucks the blood which is collected under the lengthened chin-plate, forming a little canal by means of the two extended labial palpi. Similar reductions of these particular mouth-parts can also be seen in the symphiles which are fed by their ants. Finally, all this accords well with the laziness which I observed in *Cataglyphis* laden with *Thorictus*, and may also account for the fact that this little guest is bent upon remaining attached in a permanent fashion to the ant's scape, while other *Cataglyphis* lick the trichomes at the edges of its abdomen. And therefore I now feel bound to subscribe to Wasmann's view.

However that may be, scape-*Thorictus* is much more interesting than those which simply live as guests with *Messor* or some other ant, and whose habits are little known or even unknown. I have myself made a few observations on *T. mauritanicus* with *Messor capitalis* and *striaticeps* in the province of Oran. I found it chiefly in the midst of the refuse of the seed-capsules which the ants heap up at the surface of their nests, and much less frequently inside the nest. It is never attached to the ant's scape. I have collected a very large number of these creatures, and I presume that they feed on the refuse of the granaries which *Messor* accumulates.

The scape-*Thorictus* is certainly derived from others of a more primitive kind. Is it a symphile, because its trichomes are licked, or a synœkete, because the ant supports and carries it, or an ectoparasite, because it sucks its ant's blood? Let us throw all dogmas and their categories to the four winds, and simply name it *Thorictus of the scape*.

PAUSSIDÆ

This is a large family of very special beetles, which as early as 1894, was known to include 12 genera and 165 species, 40 of which were then distinguished as co-dwellers with ants. With regard to the others, the beetle-hunters were silent: Wasmann nevertheless declares that all these species live with ants as regular guests. It is true that all the *Paussidæ* have peculiar antennæ, elbowed near the base and usually forming at the extremity a large, thick club, composed of one or several joints and assuming forms as various as they are bizarre, sometimes even armed with several teeth. Many *Paussidæ* have trichomes on the thorax, abdomen, elytra and antennæ: others have exudatory pits in place of trichomes.

I have myself found *Paussus turcicus* in Smyrna and *Favieri* in Algeria, living with *Pheidole pallidula* and *megacephala*, both right in the middle of the formicary, where they moved about majestically among the ants, in the closest intimacy with them; but I never had time to make experiments with them. Those made by Wasmann and others give us the following results:

The trichomes are licked by the ants. The curious antennæ of the *Paussidæ* fulfil several purposes:

1. Their greatest use is to enable the ants to carry the beetle about—that is, draw it along—by means of their solidity; good observers like Cardon, Gueinzius, etc., have duly verified this; the ant catches hold of the *Paussus* by the bottom of its antennæ and does not let go again until the transport is completed.
2. They protect the beetle's head against any attack on the part of the ants, and their thickness is their own protection.
3. They enable the *Paussidæ* to find by means of smell the formicaries which they are seeking or following in their emigrations.
4. They are useful to them in connection with the antennal language they carry on with the ants, not to mention the fact that they often have trichomes.

The *Paussidæ*, like the European *Brachinus crepitans*, have the faculty of bombarding their enemies from their abdomens, and in so doing they produce a perceptible noise and a little cloud of bluish smoke. When they do this on a human hand a brown spot is left behind, which is painful, sometimes even for several days. The explosive liquid smells like nitric acid and contains iodine. Kirby imagined that the ants used their *Paussus* as artillerymen to bombard their enemies in this way, while Peringuey thinks that they admit them through fear of their artillery. Both these extreme views are false and exaggerated. The admirable observations of Gueinzius have proved that a *Paussus* never bombards its ant, which drags it fearlessly along and sometimes even maltreats it; but if the common enemy which is bombarded happens to be small, it is often killed by the discharge.

A certain species of *Paussus*, *P. sphærocerus*, has phosphorescent antennæ, shining like the end of a glow-worm's abdomen, which they also resemble in the yellow colour of their last joints. Certain others, such as *P. arabicus* and *Linnæi* are treated by their ants with indifference, even with hostility. The large *Paussus hova* of Madagascar is a guest of *Aphænogaster Swammerdami*, depicted in our coloured plate I *g*.

Finally, various *Paussus* have been discovered devouring the brood of the ants which try to hide it from them. On the whole, however, the habits of the *Paussidæ*, which nearly all come from Africa, India and Australia, are but little known; their larvæ, as well as their nymphs, have seldom been studied, and we cannot tell whether they are also reared and fed by the ants.

To what category of guests do the *Paussidæ* belong? Before deciding this we must know more of their habits. Most of them seem to symphiles, but some are more like synœketes. One word of advice to those gentlemen who go beetle-hunting in foreign countries—they should be sure to take note of the attitude adopted by a *Paussus* towards its ant, and collect the two together.

AMPHOTIS

These beetles (*Nitidulidæ*), which are elliptical in form, with a flat under-surface but a convex back, seem to be true symphiles. *A. marginata*, at any rate, makes supplicatory movements with its antennæ to its ant, *Dendrolasius fuliginosus*, which disgorges honey-dew to it. The *Amphotis* is also licked by its ant. *A. Ulkei* is found in the United States, in the company of *Cremastogater lineolata* and some *Formica*.

PSELAPHIDÆ

These little beetles, with their narrow head and thorax, and large abdomen, can be considered on the whole as synœketes, forming a first stage of transition towards symphily. *Batrisus formicarius*, which is found in Switzerland as the guest of *Lasius brunneus*, has been observed by Wasmann in the act of devouring the mites which do so much harm to ants. The hosts tap *Batrisus* with their antennæ in a very friendly manner. It is the same with *Chennium bituberculatum* of Europe, which lives with *Tetramorium cæspitum* and with *Decarthron stigmosum* of the United States, which is found with *Aphænogaster fulva* and *Treatæ*.

CLAVIGERIDÆ

Very similar in form to the above, the *Clavigeridæ* are all true symphiles, and their mouth-organs are therefore transformed. Their bodies are licked by the ants, which feed them in return. In Switzerland, for instance, *Cl. testaceus* and *longicornis* are found with *Lasius flavus* and *umbratus*, whose yellow colour they have assumed. *Cl. testaceus* is blind. These insects eat ant-larvæ. Hetschko has, however, proved that they can live without their ants, as they also feed on other insects. I have myself found

Claviger, on many occasions, in the midst of the ant-colony, *longicornis* being the special guest of *Myrmica rubra.*

HISTERIDÆ

These insects, which are as hard and smooth as they are squat, are for the most part types of aggressive synechthrans, especially the large *Hister.* Nevertheless, the *Hetærius* species, such as *H. brunneipennis* of North America, which lives with *Formica subsericea* and *exsectoïdes*, have sparse trichomes which the ants lick in return for regurgitation; hence they are more like symphiles. According to Wasmann our little reddish-brown *Hetærius ferrugineus*, which is as firmly knit as it is invulnerable, is used by the ants chiefly as a plaything (by *F. fusca*, *sanguinea*, etc.). They amuse themselves by turning it over and letting it fall from between their mandibles, which slip on its hard, smooth body, since it folds its legs under its thorax and its antennæ under its head. It is rarely fed larva-fashion, but is often licked. It subsists chiefly on dead ants, but also on the brood, and lives from two to four years. Wasmann has watched it mating in the nest.

VARIOUS STAPHYLINIDÆ

The *Staphylinidæ* are a large family of beetles which has already provided us with our principal types of symphiles (*Atemeles* and *Lomechusa*), synœketes (*Dinarda*) and synechthrans (*Myrmedonia*). But it also includes a number of other ant-guests, some of which are deserving of mention.

Xenocephalus of tropical America is the guest of *Eciton prædator* and *Burchelli.* They are protected against their ants by having their head hidden under a lid-shaped thorax, which also hides their flat legs; they may also be seen running in the midst of *Eciton* armies. *Trilobitidæus* bears more resemblance to a woodlouse than to an ordinary staphylinid.

The *Oxypoda* are so nimble that they can always escape from their hosts, *Lasius*, *Formica*, and *Messor*, when pursued. They are synœketes.

Myrmecia Fussi, *plicata*, *etc.*, live near *Tapinoma erraticum* as true synecthri, in the manner of *Myrmedonia*. The *Tapinoma* ☿ greet them with a discharge from their anal glands, while the ♀ show their teeth at them, but this does not prevent the synechthran which hide in their corner and imitate the *Tapinoma* ♀, from surprising and devouring the ants. *Lamprinus* does the same.

A singular guest of the large Brazilian *Atta* is *Smilax pilosus*. It is as large as the well-known guest of our hornet (*Vespa crabro*), *Velejus dilatatus*, which is 15 millimetres long, and resembles it in shape. But it is reddish brown, and bearded like the *Atta*, and covered with a down of trichomes. Belt was the first to find it among the *Atta*. Its flat legs and its shape enable it to escape from the *Atta*; direct observations on its habits, however, are still lacking.

Homœusa acuminata, which lives with our *Lasius niger*, *brunneus* and *fuliginosus*, from a transition between the synœketes and the symphiles. The ants admit it peaceably, but rarely lick it. On similar terms, *H. expansa* and *Myrmecobiota crassicornis* of the United States live respectively with *Acanthomyops claviger* and *Lasius niger* v. *americanus*.

According to Escherich, *Oxysoma Oberthüri* of Algeria hangs on to the oily legs of *Cataglyphis bicolor* in order to lick it. I have myself observed *O. Schaumii* in the nests of *Cataglyphis megalocola*, right in the midst of the ants. Wheeler has given the name of 'strigilators' to the groups of synœketes which live by licking the oily body-secretions peculiar to some ants. On the other hand *Megastilicus formicarius* of the United States live with *Formica exsectoides* as true mimetic synechthrans. When the ant tries to attack, it sprinkles her with an acrid liquid which causes her to flee, and probably it devours the larvæ as well as the refuse. We owe these observations to Wheeler.

Finally, a whole group of *Staphylinidæ*, guests of the terrible *Dorylinæ* or visiting ants, imitate the shape, movements and sculpture of these ants so closely that they are taken at first sight for wingless Hymenoptera and not Coleoptera. Under this deceptive mask, they accompany *Eciton*, *Dorylus*, *Anomma*, etc., on their plundering raids, no doubt in order to share their prey with them, by virtue of their hypocritical shape and gestures. Among these are *Mimeciton*, *Mimanomma*, *Ecitomorpha*, *Dorylostethus*, etc. In *Mimanomma spectrum* of Kamerun the resemblance goes so far that two of the abdominal joints mimic an ant's petiole and even its postpetiole. To such an extent is this insect transformed, by regressive and parasitic phylogeny, into a 'pseudo-ant' that Wasmann was able to prove it a Staphylinid beetle only by reason of its tarsi and mouth. It probably uses the claws of its tarsi to hang on to *Anomma nigricans*, with which it lives.

Eciton prædator, of tropical America, alone has no less than twenty-seven different species of guests.

Thiasophila lives with our *Formica* and *Euryusa* does likewise, though this genus is also found with our *Lasius*. But I should never come to an end if I tried to enumerate the legion of *Staphylinidæ* living with ants.

COLUOCERA

Coluocera maderæ is a Lathridiid, and a guest of the cosmopolitan ant *Prenolepis longicornis*, which bears it with her to the tropics of both hemispheres. At Para, in Brazil, Göldi saw *Coluocera* following with its short legs upon the trail of its ant, which for her part sped upon her long legs like an arrow; he had forced *Prenolepis* to emigrate, by cementing the bottom of his terrace, the interstices of which served the ants as nests. *Coluocera* was in favour with the ants, and followed their trail exactly with the aid of its antennæ.

EMPHYLUS

These beetles, which belong to the *Cryptophagidæ*, are guests of *Formica rufa* in Europe and *sanguinea-rubicunda* in the United States, and they form a link between the synœketes and symphiles. They are sometimes licked by their ant, but they eat her when she is dead or ill.

LOMECHON

Lomechon alfaroi is a Silphid. Just as *Mimanomma* has transformed itself into an ant, so this creature has transformed itself into a true symphile covered with trichomes, not only for the pleasure of deceiving its ant, *Pachycondyla ænea* of Costa Rica, but also maybe in order to get a little quiet fun out of our friends the system-mongers, as the guest of *Anomma* did so successfully.

CETONIADÆ

It is hard to believe that many of those beautiful big golden or bronze beetles which are found on our flowers have any connection with ants. And, as a rule, it is not the Cetoniad beetles themselves, but their larvæ, particularly those of our bronze *Cetonia floricola*, which live in the nests of our *Formica rufa* and *pratensis*, half synœketes and half synechthrans. They feed on the organic débris which abounds in the nests.

Many species of the United States genus *Cremastocheilus*, however, have tufts of gilded trichomes at the anterior and posterior angles of the thorax. They live chiefly with *Formica*, and Wheeler has observed how these ants, which neither feed not lick them, properly speaking, are perpetually occupied in gnawing the anterior and posterior angles of their thorax, so greatly are they attracted to their trichomes. Moreover, the ants are incapable of injuring the hard carapace or the extremities of these insects, which are much larger than they and rectangular in form.

The genera *Plagiocheilus* and *Myrmecocheilus*, of the Cape of Good Hope, resemble those mentioned above, and seem to live in the same fashion with *Plagiolepis custodiens*, etc.

HYMENOPTERA

Most of the Hymenoptera living among ants are genuine parasites, of which we shall speak in the next chapter. Nevertheless, among those which achieve the best imitation of ants, there are some which are chiefly synechthrans. As an example I will present, in our coloured plate 1*b*, *Rhinopsis ruficornis*, which attacks *Sima rufonigra* in India, under cover of mimicry in form and colour. The striking analogy between the ant and its persecutor will probably be obvious.

Solenopsia imitatrix, a Proctotrupid, also imitates the form of our European *Solenopsis fugax*, even with regard to the two single joints of the antennal club, and lives with this ant. But as *Solenopsis* is nearly blind, *Solenopsia* does not imitate her colour and is black. This creature is probably an endoparasite which lays its eggs between the ant's abdominal rings.

Another species of *Proctotrupidæ*, *Tetramopria aurocincta*, possesses gilded trichomes and lives with our *Tetramorium cæspitum*. Wasmann therefore holds that it should be regarded as a symphile.

HEMIPTERA

Not to mention certain synœketes, of whose habits we still know very little, various special 'bugs' approach ants for the sole purpose of surprising them and sucking their blood with their probosces; these are therefore true synechthrans. Plate IV*d* shows one of these, *Dulichius Wroughtoni*, which is an admirable imitation of *Polyrhachis simplex*, the ant with which it dwells as a guest, and which is represented side by side with it in *C.* They live together on trees in India, but their mutual relations are as yet unknown.

DIPTERA

In Plate XIV (Part V) the reader will see, together with its ant, the greatest humbug among all the ants' companions. It is a mosquito, *Harpagomyia splendens*, discovered by Jacobson in Java, in the company of *Cremastogaster* (*Physocrema*) *deformis*. This curious insect's mouth is completely transformed. Instead of stinging with a pointed beak or rather with a sharp proboscis, like the mosquitoes which feed upon us, it appears with an innocent retractile mouth, analogous to that of our house-fly—thick at the extremity and designed for sucking and licking, not stinging. Instead of flying to those human beings who have no mosquito-nets, stinging them and drinking their blood (eventually communicating to them the microbe of malaria), it betakes itself quietly to some twig on a branch where its worthy *Cremastogaster* is travelling in a long procession towards the aphids it wishes to milk. There it stands still on its long legs, right in the middle of the line of ants. When it perceives or scents a *Cremastogaster* ☿ coming back from the aphids, her crop full of honey destined for the brood, the cunning mosquito lowers its legs and taps the ant's head with its antennæ in a manner as friendly as it is sly. Deceived by appearances, the ant regurgitates honey-dew by a habitual reflex movement, and the artful creature quickly swallows it, and the process then begins again. This honey-dew is an advantageous substitute for human blood, obtained without danger, and serves to mature the eggs which will certainly be laid soon after in some marsh.

Under what heading are we to place these thieves ? They are not symphiles, since they do nothing but steal; they are not synœketes, since they do not live in ant-nests; they are not synechthrans, since they do not attack or kill any creature; they are not parasites upon either the inside or the outside of the body. They are simply amiable robbers. They take from the ants, in a friendly manner, what they have extorted from the aphids, which in their turn have drained it out of the plants. In the long run, it is the plants alone which are robbed. O Holy Mother Nature, how tortuous are thy ways! I therefore baptize *Harpogomyia* with the name of *synclept* (robber with).

Another of the Diptera, *Microdon mutabilis*, lives in its larval stage with several of our *Formica* (*fusca*, *rufa*, etc.), and our *Lasius* (*niger*, *flavus*, *brunneus*), which treat it like the large coccid it strongly resembles. *Microdon* has a certain kind of trichome, which according to Wasmann is licked by the ants. The various species of *Microdon* live with numerous genera of ants in Europe, America and Australia. Wheeler has searched in vain in his apparatus to discover what these larvæ live upon. The perfect insect, however, soon flies away out of the ant-nest.

MYRMECOPHILA

The *Myrmecophila* are Orthoptera of the cricket family, living among ants. These delightful and agile little insects, which leap like our crickets, but have no wings, are found in Europe, North Africa, India and the United States. *M. acervorum* lives chiefly with our *Formica* and *Myrmica*. But its young forms or larvæ, which also leap, are found with the smaller genera, *Lasius* and *Tetramorium*. In the south they are found with *Camponotus*, etc., in India with *Bothroponera* and *Plagiolepis*. *M. ochracea* is found with *Messor barbarus* and its little larvæ with *Pheidole*. In Tunis I have taken *M. Salomonis* with *Monomorium Salomonis*. *M. Pergandei* is found in the United States, especially among certain *Formica* and *Camponotus*.

The *Myrmecophila* are true strigilators. They are perpetually licking the oily secretions on the bodies and limbs of their ants, which they caress the while with their antennæ. In return, they clean the nest in an admirable fashion and devour the mites which infest it and destroy the ants. The *Myrmecophila* are comfortably lodged by their hosts, but they do not receive honey-dew by regurgitation. On the other hand, the secretions which they lick from the ants help to feed these miniature crickets.

Silvestri has proved, however, that *M. ochracea* sometimes eats the larvæ of *Messor*, though the innocent *M. acervorum* does no such thing. In Bombay, Assmuth has seen *M. prenolepidis* following *Prenolepis longicornis* while it is changing its quarters, at the same time as *Coluocera*, which we discussed above. Like this same *Coluocera*, *M. prenolepidis* has followed its ant to Brazil. Here, therefore, guest and ant are both cosmopolitan.

Wheeler has observed very correctly in his artificial nest, the skill with which the little *M. nebraskensis* licks the legs of its fearsome ant, *Pogonomyrmex molefaciens*. In short, the *Myrmecophila* lives in true syndiacony with its ant, especially *M. acervorum*. Some of them should rather be termed synœketes.

ATTAPHILA

The *Attaphila* are little cockroaches (*Blattidæ*) which live with the leaf-cutting ants, the *Attini* of tropical and subtropical America; that is to say, in their fungus gardens. Wheeler has observed them in his artificial nests. They do not eat the fungus-gardens, but climb on the backs of their ants and lick them. These creatures are strigilators. The ants do them no voluntary harm, but while browsing in their fungus-gardens they often accidentally cut off a few joints from their antennæ.

A. fungicola lives in this manner with *Atta texana* of Texas. In the Argentine, *A. Bergi* lives similarly with *Acromyrmex Lundi*. According to Bolivar, this species climbs on the back and even the head of the winged ♀ and ♂, but never on the ☿. After the nuptial flight it remains perched upon its ant, which carries it away into the air.

LEPIDOPTERA

Certain moth caterpillars, those of *Myrmecocela ochraceela*, for example, live in the nests of ants (*F. rufa*) and dine upon their rubbish-heap. Others, like those of *Psecadia decemgutella*, are reared, according to Thomann, in the Cantons of Grisons by *Formica rufibarbis*, etc.

Others, however, belonging to certain Lycænids, are used by the ants as food, and accordingly we shall discuss them together with the aphids, etc., in Part III. Similarly, the parasitic ants which are guests or slaves of other ants will be dealt with in the next two parts. Here ends, therefore, our account of the principal insects which are ant-guests in the broad sense of the word. I have omitted a large number to avoid wearying my readers, and because they are less interesting or little known. But we have still a few words to say about other animal guests which are not insects.

THYSANURA

The *Lepisma*, first on our list, are silvery little animals which run swiftly, and are often seen in our homes among the flour. Several of their species are ant-guests. I have myself found among others numerous *Lepisma Foreli* and *Wasmanni* living in the nests of *Messor barbarus* and *arenarius* in Algeria, where they seem to me to be pure synœketes, scavengers of the débris in these ants' granaries. They live inside the nest. *L. aurea* does the same in southern Europe.

Atelura and *Lepismina* do more than this. They watch two ants regurgitating honey-dew to each other; they then rear themselves up on their legs and secure part of the regurgitated drop, at the same time tapping the ants in a friendly way with their antennæ, as shown in fig. 37 (after Janet) in the case of *Atelura formicaria* and *Lasius mixtus*. I have myself taken *Lepismina* in large numbers in Smyrna in the company of *Cataglyphis viaticus - orientalis*. For this reason I was taken for a sorcerer in the Turkish quarter, and they threw stones at me until I was forced to withdraw.

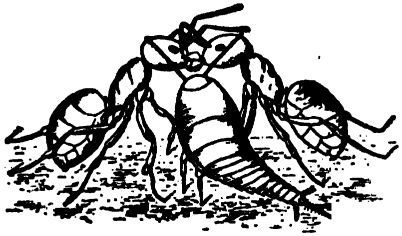


Fig. 37

SPIDERS

Some spiders live in ant-nests—for example, the little *Walckenæra* lives as a synœkete with *Formica rufa*. It is not yet very clear what they eat. Most of them, however, are mimetic synechthrans which lie in wait for ants near their nests, attack them singly and eat them. I have seen specimens of several foreign species which imitate marvellously the form and colour of *Œcophylla*, *Polyrhachis*, and even *Harpegnathus* (Part V, plate 1*k*). Our European *Theridium* causes great slaughter among *Formica rufa*, which it enmeshes in its web and afterwards hangs.

MITES

Many of these mites are simple parasites, of which we shall speak in the next chapter. *Lælaps*, however, is a true inoffensive synœkete, living on the offal of ant-nests. *L. oophilus* does not eat ant eggs, but settles on them in order to take advantage of the ant's secretion when she licks them; this is what Wasmann calls syntrophy (feeding with).

Antennophorus pubescens and *Uhlmanni* are more mischievous. They perch under the ants' heads (as shown in fig. 38), stroke them with their front legs, which imitate the movement of the antennæ, and thus succeed in making them regurgitate honey-dew. This is a veritable caricature of symphily, but in miniature. The ant (*Lasius mixtus* in this case) vainly makes her utmost efforts to rid herself of this troublesome parasite, which takes such an unfair advantage of her reflex movements to gorge itself with honey-dew; but she does not succeed without the aid of a *Dinarda* or one of the other obliging synœketes.

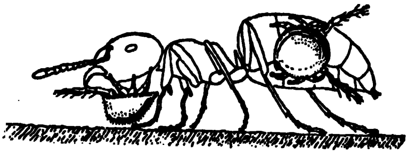


Fig. 38

Glyphopsis formicariæ imitates *Claviger* (a beetle guest). Although it is a simple mite, it indulges in trichomes, and thus appears to be a symphile licked by the ants. But I am quite sure it repays itself by sucking juices from some part of the ant's body.

MYRIAPODS (*millipedes*)

Many woodlice, including *Porcellio scaber*, live with *Formica rufa* and other ants. But one of the most common among countless species of our European *Formicinæ* and *Myrmicinæ* is *Platyarthrus Hoffmanseggi*. This white millipede is found inside formicaries at all stages of its growth. The ants pay no attention to it, but neither do they do it any harm. It is always moving about; but what it lives on, or what it does there, we do not yet know.

In concluding this long chapter, whose contents we owe mainly to Wasmann, we may say that this author has clearly shown how several guests of termites, by phylogeny, are descended from certain myrmecophilous (ant-loving) guests of the *Dorylinæ*. He thinks that this was brought about as a result of the invasion of the termite nests by armies of these visiting ants, since the guests of the *Dorylinæ* usually ride on the backs of their ants as we ride horses.

Chapter V

PARASITES, TOXICOLOGY AND ANT-MONSTROSITIES

1 ECTOPARASITES

BEETLES

Parasites living upon the surface of the ants' bodies come next in order and form an insensible transition from the guests we have just discussed. *Thorictus*, for example, which as we have seen sucks the blood from its ant's scape, is as much an ectoparasite as a symphile, but it is almost the only beetle so circumstanced, apart from the larva of *Clythra*. This creature independently encloses itself in a little barrel of damp earth, and walks about in this condition on its front legs, inside the formicary. As soon as an ant comes near it, it stands still and draws its legs under the barrel, which seems to the ants a promising place for their eggs. Then, directly they go away, the *Clythra* larva pops its head out and devours the eggs. The ants see nothing of this.

DIPTERA

In Java, a little fly named *Bengalia latro* has the impudence to take up its position on some hillock near *Pheidologeton* (Part I, p. 32, coloured plate III, *a*, *b*, *c*,), which files by; it then swoops down like a falcon upon an ant which it detects with its great eyes, and still on the wing, snatches away the the prey which the ant is carrying. Jacobson, who has often seen this happening, says that he finds it hard to understand how the fly, which, moreover, is more like a simple synecthran, always escapes from the ants.

Fig. 39 represents *Metopina Pachycondylæ*, observed by Wheeler in Texas, with the warrior-ant, *Pachycondyla harpax*. This insidious little fly lays its eggs on the ant's larvae. Directly it is hatched, the little *Metopina* larva encircles the neck of the ant-larva as in fig. 39, and stretches its beak towards that of the larva. As soon as a ☿ *Pachycondyla* gives its larva food, in the form of slain insects, the little *Metopina* larva takes its share without doing any harm to its host; and when the latter eventually spins itself a cocoon, the *Metopina* larva does not hinder it and allows itself also to be enwound. It then humbly ensconces itself at the end of the ant's abdomen, in order to turn into a nymph in due course. It is thus protected from the mandibles of the adult ant, which later comes to open the cocoon. At that moment, the *Pachycondyla* is hatched, and the open shell is thrown on the refuse-heap. But the *Metopina* is also hatched on the refuse, and then flies away. While still a larva, it sometimes pinches the neck of the larva it is encircling, in order to make it to move. This causes the adult ants to feed it again. Otherwise, the ants do not suffer in any way by reason of this little robber-parasite. These examples are sufficient.

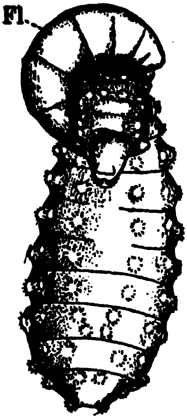


Fig. 39

HYMENOPTERA

Orasema viridis, a pretty little Hymenopteron, lays its eggs on the adult larvæ of *Pheidole instabilis* of the United States, and afterwards devours the nymph by sucking so much substance from it that it might be taken for a consumptive. In the end, nothing remains of it but the skin, and the *Orasema* transforms itself into a nymph in its place, hatches and flies away.

I once had sent me from Australia several specimens of the enormous *Myrmecia pyriformis*, which is 2½ centimetres long, together with their cocoons. When I opened these cocoons, I discovered *Myrmecia* nymphs inside some of them, and in others the nymphs of a large and splendid hymenopteron of a lustreless golden-green, with brown abdomen. They were mature and ready to hatch; I sent them to P. Cameron, who described them as a new species: *Eucharis Myrmeciæ*. This was evidently analogous to the case of *Orasema*.

MITES

Among the numerous little mites which plague ants, we have already mentioned, under the category of guests, *Lælaps* and that little humbug *Antennophorus*. *Cillibano comata*, described by Janet, is more distinctly an ectoparasite upon *Lasius mixtus*. It attaches its antenniform legs, as well as its beak, to the abdomen of *Lasius*, and makes scars there through which it evidently sucks the ant's blood.

Uropoda philoctena attaches itself to the front legs of this same *Lasius mixtus* with the aid of a sticky secretion, climbs on to the ant's spur, takes a firm hold of the point, and thus feeds on the more or less oily impurities which the ants comb from their own bodies, between the comb of their spur and the brush of their tarsus which we saw in fig. 9 (Part I).

I will spare my readers any further examples; these will suffice to explain ectoparasitism.

2 ENDOPARASITES

HYMENOPTERA

Certain Braconids, *Elasmosoma berolinense* and *viennense*, while on the wing, relentlessly pursue *Formica*, *Lasius* and *Camponotus*, until they succeed in laying a parasitic egg under a segment of their venter, curving back their own abdomen. As early as 1873, chiefly in the course of the wars which these ants carried on among themselves, I observed this Braconid buzzing over the combatants, striving to reach their abdomens. The ants defended themselves by turning round and biting, and they generally managed to drive the parasites away. But nothing would induce the creatures to cease; they always began again, and so did some little Phorid flies, still smaller than they, which imitated them. I then noticed that neither *Elasmosoma* nor the fly ever settled upon dead or sick ants; they had designs on the healthy ones only.

DIPTERA

We have just mentioned the little Phorid which pursues our ants. Being more adroit than *Elasmosoma*, it more often succeeds in settling on an ant's abdomen. Its own venter, which ends in a mobile point, can easily be curved so that a parasitic egg may be laid under one of the abdominal segments of its victim, as in the following case:

In Limburg, in August, Wasmann saw another Phorid, *Pseudaceton formicarum*, pursue some *Lasius niger* like a falcon, and perch for an instant on their abdomens. The *Lasius niger* only noticed it at a distance of about a millimetre, and then she defended herself. The fly is partly directed by smell, for it also came and settled on Wasmann's hand; which was impregnated with the odour of *L. niger*. Wasmann had no better success than I in finding the egg laid by this fly, which is only 1·17 or 1·4 millimetres long.

On the other hand, Coquillet has seen a Phorid in Brazil, *Plastophora Crawfordi*, whose ♀ is wingless and lives with the ants, laying its eggs on the head of *Solenopsis geminata*.

The Phorids *Commoptera Solenopsidis* and *Ecitomyia Wheeleri* in America, in addition to their parasitism, have glandular exudations which are licked by the ants, so that they may the more easily lay their eggs on *Solenopsis* and *Eciton*: a touch of hypocritical symphily wins the day!

But to crown all, dear reader, I will introduce to you *Apocephalus Pergandei*, which was discovered in the United States by my late friend Pergande. This Phorid openly attacks the big worker of the large *Camponotus pennsylvanicus* and gives her neither quarter nor respite for hours at a time, until it has contrived to lay an egg in her neck, between the head and the pronotum. The ant has then received her death sentence. Once the egg is laid, the little larva of the Dipteron creeps in above the prosternum and into the ant's big head, where it devours the living muscles and brain. Pergande observed all the stages of stupefaction in such unfortunate *Camponotus*, which at first wandered pathetically about their nests, and then remained motionless, hanging their ever emptying heads. At last, when the larva has devoured everything that is edible, it finishes its work in this way: Before turning into a nymph, it cuts the last ligaments, which were still fastening the ant's head to its thorax, and thus entirely decapitates the *Camponotus*. The head then falls off, and provides the *Apocephalus* with a cocoon as safe as it is comfortable. After hatching, it flies away and leaves the remains of its victim in order to find fresh ones.

NEMATODES

The nematodes are true still-worms, like the earth-worms and some of those which also delight to live as parasites in our intestines; hence they are neither larvæ about to

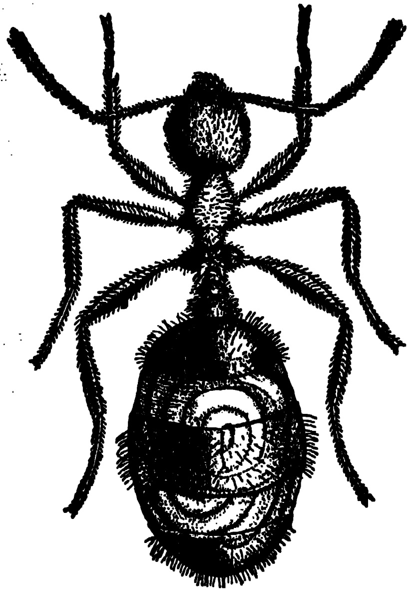


Fig. 40A

become ants, nor caterpillars about to be transformed into butterflies. Fig. 40A shows a gigantic ☿ *Pheidole commutata* from the United States, whose swollen abdomen is filled with the convolutions of a large nematode of the genus *Mermis*. This ☿ has a tremendous head provided with ocelli, and Emery once took the head of an analogous species received from America for that of an ergatogyne replacing the ♀ for the time being. But Wheeler proved in due course that all individuals such as this contain *Mermis*, and he baptized them *Mermitergates*, which means 'workers with Mermis.'

Fig. 40B

He thinks that the *Mermis*, which is apparently present even in the ant-larva, stimulates its appetite to such an extent that it grows, and its ontogeny varies so far as to produce some degree of resemblance to a ♀. *Mermis* certainly lives inside the ant's crop.

Fig. 41 *A* and *B* shows a similar transformation in the worker, also due to *Mermis*. This transformed worker *A* also has ocelli, but instead of growing large like the *Pheidole*, she

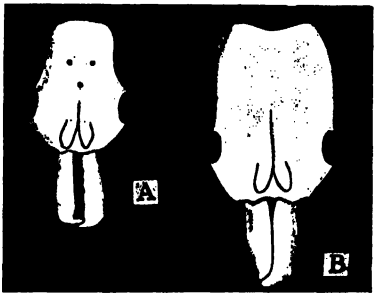


Fig. 41A and B

has a head which is very narrow at the back; compared with the normal worker *B* her figure has not increased. Whether she ate less as a larva than *Pheidole commutata* is a question for Wheeler to answer. The abdomen is swollen by the crop, like that of *Pheidole*. These facts have also been observed and discussed by Emery.

Janet saw a nematode several centimetres long come out of the labial gland of *Formica fusca*. De Man then described under the name of *Pelodera Janeti* a strange nematode which passes its first stage in the pharyngeal gland of *Lasius* and *Formica*, suffused in the glandular secretion, which serves it as food. This parasite afterwards comes out of its gland and through the mouth of the ant, which does not seem to have suffered greatly by its presence. The *Pelodera Janeti* afterwards feeds freely upon the refuse of the ant-nests, and gives birth to a series of generations which continue to live freely without returning to the glands of our little friends.

Your brain, dear reader, must be reeling over ant-guests and ant-parasites, and so I will stop; but do not give way to melancholy as you read of the actions of these mutual devourers or thieves. Remember that we men and women are no better than they. Think rather how we ourselves, though remaining synechthrans to the animals and plants we eat, or at least synœketes to some of them, might contrive to become more honest symphiles to our fellow human beings than we have hitherto been throughout the world, and cease to exploit them—as far as possible, at any rate. And, therefore, let us aspire to a true international human syndiacony, in place of our present hypocritical symphily.

3 Toxicology of Ants

Toxicology is the science of intoxications. But have no fear, dear reader, that I am proposing to inflict on you a long scientific treatise on blood-poisoning in ants; for that matter, I am incapable of so doing. But a few facts may interest you, and this in the first place—that the poisons known to us generally act on them quite otherwise than they act upon ourselves. A few examples will enable you to judge of the matter.

Action of corrosive sublimate. Belt (*The Naturalist in Nicaragua*, London, 1874), tells how, in dry weather, he sprinkled some corrosive sublimate powder across the path traversed by one community of *Atta sexdens*, and brought about a general conflict. All the ☿ rushed furiously about, attacking and killing one another. My curiosity led me to check this fact, and at Munich on August 21st, 1876, when the weather was very dry, I sprinkled some powdered sublimate on a nest of *Myrmica scabrinodis*, the domes of which I had just opened. After a few moments, the ☿ began to seize hold of one another, curling up their abdomens. One of them took a male and carried him far away from the nest. Others dragged the first companions they encountered (among others, some that were newly hatched) into the surrounding grass, so as to take them as far away as possible, and finally to release them as ants release their enemies in the cold-blooded combats of which we shall speak later. Chains of three or four ants were formed; in a word, the peaceful harmony of the formicary was instantaneously transformed to reciprocal aversion among all its inhabitants, and the aversion degenerated into brawls and struggles. After a few moments, however, the scene grew calmer; after a quarter of an hour, all the ☿ slackened their efforts and ceased to fight, and order was re-established. A similar experiment with *Lasius niger* and *flavus* gave no result; the ants did not notice the presence of the sublimate. On the other hand, when repeated with the same *M. scabrinodis* on a fairly damp day, it had the same effect as on the dry day. The action of the sublimate varies, therefore, according to the species, and there is no cause for doubting the accuracy of Belt's account of the violent combats which it produces in *Atta sexdens*. We must assume that the sublimate has an action upon the nervous system of *Atta* and *Myrmica* (probably through the sensory organs of the antennæ), which disturbs their faculty of recognising one another and makes them take their companions for enemies.

But here lies the explanation. When the antennæ of various *Formicinæ*, *Lasius*, *Formica*, *Camponotus*, etc., in different colonies are cut off, they behave like the animals in Paradise, and all eat together in perfect peace out of the same bowl. But the *Myrmica* species are different. These do the opposite—they fly into a temper and attack all the rest of the menagerie, as I proved later on in 1886, when I confirmed my supposition of 1876 (see Chapter I, p. 190, smell).

It is obvious, therefore, that the effect of amputating the antennæ is similar to that produced by the sublimate, but that it varies with the different sub-families. How is this to be explained? What is the cause of the idyllic peace reigning over the *Formicinæ* and the bellicose fury of the *Myrmicinæ* when both have ceased to recognise their relationship? Doubtless it arises from the momentary paralysis of topochemical smell by the sublimate. My *Myrmica* with the antennæ cut off also became quiet in the end, for that matter, but the difference between their primitive re-action and that of the *Formicinæ*, with respect to both the sublimate and the amputation of both antennæ, remains inexplicable. The amputation of a single antenna has no such effect.

I have made still further experiments. Opium and morphine, instead of sending ants to sleep as they do us, give them cramp. *Formica pratensis* will eat honey which has been mixed with phosphorus; but they afterwards fall ill and remain for a few days with their mandibles open (see Chapter I), almost motionless, and looking as though they had bad pains in their stomachs, or in other words, their crops. Some of them die; others recover quite unaided, without medicine or drugs. Furthermore, I have seen various ants gorge themselves with honey containing arsenic without suffering in the very least thereby, whereas Persian powder kills them.

There is room for some interesting studies in comparative toxicology. One day, perhaps, someone will thus discover a means of destroying *Lasius emarginatus* and *Iridomyrmex humilis*, which infest houses and make their nests between the stones of their walls.

HERMAPHRODITES AND MONSTROSITIES IN ANTS

I HERMAPHRODITES

By hermaphrodities we mean creatures which are at the same time male and female. In certain animals hermaphroditism is normal, for example in the solitary worms which fertilize themselves, or the snails which mutually fertilize each other as they embrace. In both cases, each individual bears normally in its own person the two kinds of sexual organs, ♀ and ♂.

In the seminal vesicle of the ♀ ant, pictured in fig. 19 (Part I), and described in Chapter IV (Internal Anatomy), we have learned to recognize a curious secondary hermaphroditism which is likewise normal.

But in all animals which allow themselves the luxury of developing separate and differently sexed individuals, primary hermaphroditism cannot be normal. It is replaced by copulation, except in cases where the ♀, doubtless through nature's economy, sometimes substitute for it parthenogenesis by means of eggs which develop without being fertilized. This also takes place in ants.

Primary hermaphroditism among ants, therefore, is abnormal, or in other words, pathological; it is included among the monstrosities. But, in their case, it offers many peculiarities due to the sometimes enormous polymorphism of our little friends. In the first place, it can take place not only between ♀ and ♂ but also between ☿ and ♃, as anyone can easily distinguish at a glance, owing to the great polymorphic differences in form and colour.

In the second place, hermaphroditism affects not only the organs themselves, but all the corresponding peculiarities of the rest of the body: shape, wings, colour, eyes, number of joints in the antennæ, etc.

In the third place—and this is very curious—hermaphroditism may be lateral, one side of the body being ♂ and the other ♀ or ☿, or oblique, or cross-wise, or combined, or mixed, sometimes even really double. Examples and figures such as we give here teach more in this respect than any amount of theorizing.

First of all I present a lateral hermaphrodite belonging to *Azteca Mülleri*, partly ♂ and partly ♀. I myself received it some time ago from Sta. Catharina, Brazil. Its head is represented in fig. 42. The

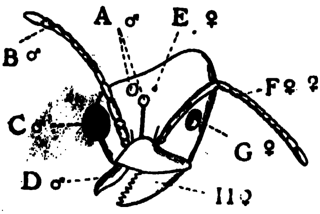


Fig. 42

left half of the figure (right of the ant) is ♂, the other half is ♀. Now the normal ♂ measures scarcely 3·5 millimetres in length, and the ♀ more than 10. The hermaphrodite measures 4·5. *D* shows the little toothless ♂ mandible, *H* the large toothed ♀ mandible, *C* shows the large ♂ eye with its numerous facets, *G* the small ♀ eye. Between the two we notice a somewhat distorted combination of the small ♂ epistoma and the large ♀ epistoma, which is concave only along its upper edge. The ♂ antenna, *B*, has only a very short scape, but 13 joints, while the ♀ antenna, *F*, has a long scape but only 12 joints. The vertex has a small lateral ♀ ocellus *E* and and a large lateral ocellus *A*. The largeness of the median ocellus *A* denotes that it is ♂. The thorax is also half ♂, half ♀, as well as the two pair of wings. On the other hand, the abdomen, whose gizzard I have succeeded in dissecting, is entirely ♂ externally, and this explains the small size of the ant in question. This simple example alone takes us farther than the longest theory. It was on this that I founded my description of the normal ♂ in *A. Mülleri* and the genus *Azteca*, but later on I received the whole normal ♂ himself.

Secondly, in fig. 43, we have a hermaphrodite between the ☿ and ♂ of a *Polyergus rufescens*, which is in my *collection* and which I myself found some time ago at Vaux near Morges. In this species the ♂ is black and the worker is reddish-brown. The mandibles (*D*,*G*), the antennæ (*C*,*F*), eyes (*B*,*E*) and ocelli (*A*) correspond fairly well to

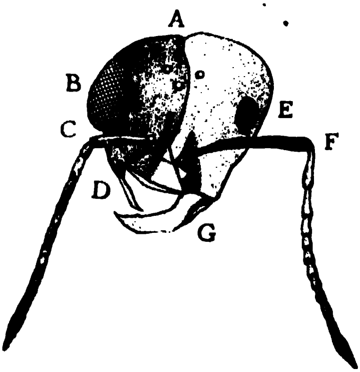


Fig. 43

those of fig. 42, but the arched and pointed mandibles of the slave-making worker lack the teeth of the ♀ *Azteca*, The pronotum is ☿, except for two ♂ spots on the right. The left of the mesonotum is that of an apterous ☿ and the right that of a ♂, with crumpled wings and half a scutellum. The epinotum and pedicel are ☿, except for a few ♂ spots on the left. The right legs are half ♂, the left ☿. The external abdomen is entirely ☿.

Thirdly, in fig. 44, we have the internal genital organs of another hermaphrodite, a *Polyergus rufescens* of the same colony, which I took after an expedition during which I saw it rifle and carry away to its nest a *F. rufibarbis* larva, along with the ☿ its companions. On its left side (*ov.*) is a simple little ovary. On the right, however, we have a testicle *t.* at the top, coupled with a little ovary, *ov.*, then a seminal canal, and near the bottom a ♂ seminal vesicle.

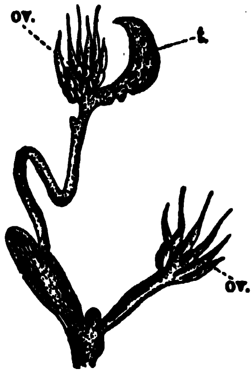


Fig. 44

Right at the bottom, these organs end in an uneven canal which may be called a vagina, natrix or ejaculatory duct, according to taste. It really leads to a complete pair of irreproachable ♂ genital valves, like those depicted in *G*, *H*, and *I*, fig. 10 (Part I).

But most interesting of all is the fact that this creature's head and prothorax are entirely ☿—reddish-brown, except for a black spot under the throat. It is evident, therefore, that the brain was entirely ☿, which explains the slave-making tendencies. The mesothorax, the metathorax, the four back legs and the scale are ☿ on the left and ♂ on the right, with a very sharp median line of demarcation, and wings on the right. The three first segments of the abdomen are also ☿ on the left and ♂ on the right. Segments 4-6, on the other hand, are entirely ♂ ; the sixth is small and defective, except for a genital valve. Finally, attached to the whole, we have a rudimentary poison vesicle without a distinct pad.

Formica rufibarbis.—This creature is extremely curious. The characters of two sexes are closely intermingled on both sides at the same time. The two sides of the head are perfectly identical, and yet it is impossible to say whether this is a male or female head; its form is exactly intermediate between the two. The two antennæ are 13-jointed, as in the ♂, but the scape is longer in comparsion with the funicle. The two mandibles are indistinctly dentate, and of a mixed reddish and brown colour; it is hard to say whether they are ♂ or ♀. The ocelli and eyes are also intermediate in form and size. The whole head is stronger than that of the ♂, and weaker than that of the ♀; and black in colour. The thorax is indeterminable; the most striking thing about it is that the right half of the epinotum is yellowish-red, and the left half black, while the right half of the scutellum and scale are black, and their left half is a yellowish-red; the metanotum is ♀ on the right, ♂ on the left, whereas the scutellum and scale are ♂ on the right and ♀ on the left. The six legs are symmetrical and yellowish, and predominantly ♀ in shape. The wings are identical with each other. The abdomen seems to be ♀ ; it has five segments (not counting the scale) and is globular and somewhat small. The cloaca is round, and surrounded with hairs, as in the ♀, but opens at the top into a transverse, non-ciliated slit, situated between the hypopygium and pygidium, and constituting a kind of second cloaca. The true cloaca is formed out of the hypopygium. I took this hermaphrodite on the wing, at the top of Monte Salvatore, in Ticino. It was accompanying some ♀ and ♂ of its species on their marriage-flight. This seems to denote a reproductive instinct.

After removing its *poison vesicle*, which was quite recognizable and almost normal in shape, but short and compressed with a small pad, I found on the left of the stomach a perfectly normal ovary, with a sheath full of eggs, it was ♀ in shape, but very small. On the right, slightly towards the middle, and somewhat superficially placed, was a curious little organ, evidently rudimentary, although I could not explain its significance. It had the form of a very blunt cask. Near the cloaca it was very difficult to recognize, but the rudiments of chitinous organs (possibly genital valves) were present.

Formica truncicola. This is an irregular combination rather than a mixture; the left half is predominantly ♀, but not entirely so. The abdomen has a ♂ appearance externally, with typical ♂ genital valves on each side. The interior is similar as regards the ♂ organs. But there is also a distinct ovary underneath, smaller than the ♀ ovary, but larger than the ☿ ovary, containing a number of eggs. None of these eggs, however, is mature on the under side. Another supplementary horny organ seems to me to be a rudimentary poison vesicle.

The most interesting point about this case is the fact that it is a true ♂ and ♀ hermaphrodite; a complete ♂ on both sides and a ♀ on one at least. It is no less abnormal for that.

Formica exsecta.—This is a ☿ which has some ♂ portions on the left side, but the ordinary contour of a ☿. The male parts are: (1) a longitudinal black band under the left side of the throat; (2) the left half of the pronotum; (3) a large black, V-shaped spot on the left side of the mesonotum, where there are also a black protuberance (scutellum ?) and

Nest of *Cremastogaster* (*Oxygyna*) *Ranavalonæ*. Madagascar.

the rudiments of wing-articulations. All the rest is ☿. The mesonotum is malformed.

In 1903 Wheeler described various other interesting cases analogous to mine, reviewing at the same time the cases which had previously been described. Here once more let us set aside all the hypotheses which claim to explain but only mislead. Certain new facts, however, must not be passed by in silence.

It was irrefutably established by Bouin and Ancel between 1903 and 1912, and more particularly by Steinach in 1910, that during adolescence in birds, mammals and men, we can masculinize a female and feminize a male by transplanting ♂ sex-glands to the first and ovaries to the second. A hen then acquires the feathers of a cock, and *vice versa;* an Indian boar acquires mammary glands and suckles the young of a companion; a homosexual person is cured, etc. And feelings likewise are masculinized or feminized accordingly to the quality of the sex-gland grafted. These are not stories from the Thousand and One Nights, but definite facts, which I have seen recorded in photographs lent me by M. Lipschütz, the author of a great work on this subject.

Our problem is now to discover what deeper, common ontogenetic cause connects these facts concerning the transplantation of ♀ and ♂ sex-glands by surgical operation with the no less certain facts which we have just learnt in connection with ants. The transplantation facts demonstrate the chemical action of gland-secretion, and how it spreads over the further ontogenetic development of the entire individual, physical and mental.

But what is the origin of hermaphrodites, lateral, crossed or mixed, with which we have just become acquainted? Here I shall content myself with asking the question. Others will reply. It is probable that primordial anomalies of the egg after its fertilization, or even before, may play a large part in the matter.

2 TRUE MONSTROSITIES

Hermaphrodites, especially where only one part of the body is affected, such as a ♂ *Myrmica* with a long ♀ spine on the right side of its epinotum, are essentially true monstrosities; and all these monstrosities are, like hermaphrodites, of ontogenetic origin.

The most curious specimen I possess is a ♂ *Hypoclinea quadripunctata*, with seven legs and five wings. To begin with it has six normal legs and four normal wings, with the corresponding thoracic sclerites, also normal. The left lateral posterior edge of the pronotum bears a small adventitious piece, round and chitinous, to which is jointed the fifth wing, rudimentary and somewhat crumpled. This sclerite is slightly below and in front of the articulation of the upper left wing. On the left are four legs; the three back ones are the normal legs, for the second bears the typical spur, and its structure conforms perfectly to that of the anterior right leg. The anterior left leg is therefore the adventitious one; it is perfectly formed, with normal tarsus, tibia, thigh and haunch, but it has no typical (pectinate) spur. Fearing to damage the insect, I have been unable to ascertain definitely the manner in which this adventitious leg is jointed to the *prosternum*. The rest of the body of this male is perfectly normal. I took it on the wing at Busigny (Vaud).

In one of my artificial *Leptothorax acervorum* formicaries, I observed a ☿ walking with her abdomen held very stiffly and inclining to the left. She was shorter than the others, but worked like them, carrying larvæ, etc.; and she was incapable of moving her abdomen upon her thorax to any appreciable extent. This was due to the fact that the pedicel was firmly fused to the metathorax, forming one piece with it; it was also atrophic, with no sign of a division into two nodes; and its articulation with the abdomen was arranged at a slightly oblique angle, and scarcely movable at all. The *epinotum* itself was deformed and spineless. The rest of the body was normal.

These examples will suffice. In our previous chapter (IV), we discussed the pseudogynes depicted in fig. 33 and caused by the presence of *Atemeles* and *Lomechusa* (see Symphily). I do not wish to deal with them again. A glance at the figure will suffice to show that this degenerate, hunch-backed creature is neither ♀ nor ☿, but simply a wretched caricature of both. It is also an ontogenetic monstrosity. We may bring this chapter to a close with the remark that ants, like ourselves, have their monstrosities and their acquired as well as hereditary diseases. I will venture to add that such anomalies seem to be more frequent in colonies reared by means of artificial apparatus than in natural colonies—just as is the case with our own domestic animals and plants, compared with savage creatures.

Chapter VI

ANT-NESTS

Where do our little friends build their nests ? 'Everywhere' is the reply, as will soon appear! But I have no wish to describe here the artistic activity of ants, the manner in which they build or construct their nests, roads, stations and branch-establishments. I reserve these matters for Parts III and V; and at present I shall simply show the nests just as they are. The rest concerns habit, and I wish to avoid too much repetition. A few preliminary remarks are none the less necessary.

In the first place, ants are not like bees and wasps, which build their nests out of wax or carton and form polygonal cells whose structure is instinctively fixed for each species by heredity. Ant-nests, on the contrary, are nearly all *irregular*, *variable* and *adaptable* to circumstances. True, they often have specific characters, but these are rarely altogether fixed.

Secondly, I had better refer you to Pierre Huber; *Les Fourmis indigènes* (second edition, Geneva, 1861), and the second edition of my own work, *Les Fourmis de la Suisse*, (La Chaux-de-Fonds, 1920, Part III, p.62) for further details as to the architecture of the nests made by Swiss and French ants. We shall deal here with those made by ants all over the world. Even with this restriction, our subject is nevertheless fairly large.

Finally, I will recall the fundamental distinction I made between the terms 'nest' and 'formicary.' The formicary is the whole social unit, bound harmoniously together; it may possess several nests, and is then known as a *polycalic colony*. The nest is the habitation of the ants: it may contain several formicaries, and is then known as a double, triple nest, etc.

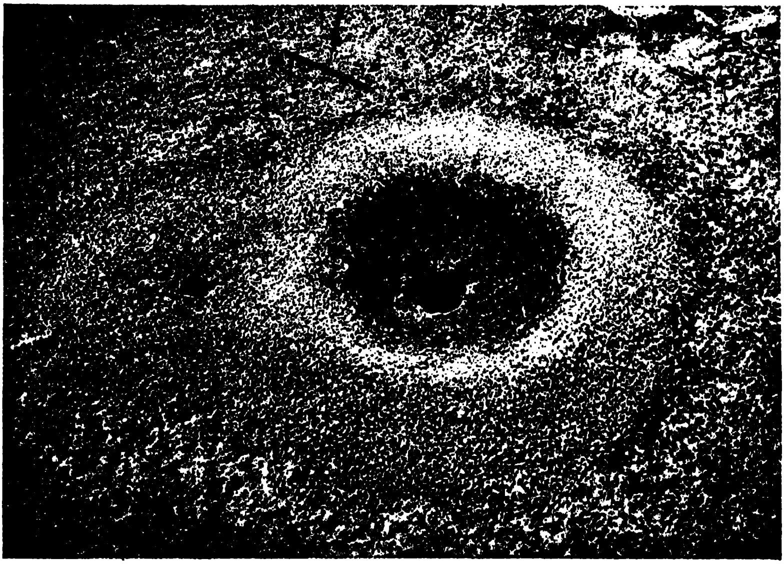


Fig. 45A

A NATURE AND ARCHITECTURE OF NESTS

I NESTS IN EARTH

In Europe, most ants live in the earth; in the desert, they live in sand, and in virgin forests, on or in trees. Nests constructed in the earth can be divided into three categories.

a NESTS SIMPLY DUG OUT.—Ants of the following categories, *b* and *c*, often make simple subterranean nests, especially in dry warm countries and in any place where a young or weak colony is trying to escape from enemies which threaten it. In that case, the ant which digs in the earth with its mandibles, is content, when it comes out of the hole thus made, to carry away to as great a distance as possible the earth that has been scooped out, and to conceal the entrance of the nest, either by placing it under a tuft of grass, or by making it as small as possible, or even by blocking it up with scraps of earth. The subterranean nests are composed of galleries and chambers formed in the earth and are either dense, that is, placed near one another, or distant, that is, scattered, according to species and circumstances. The ramifications of subterranean nests may sometimes extend for a very long way.

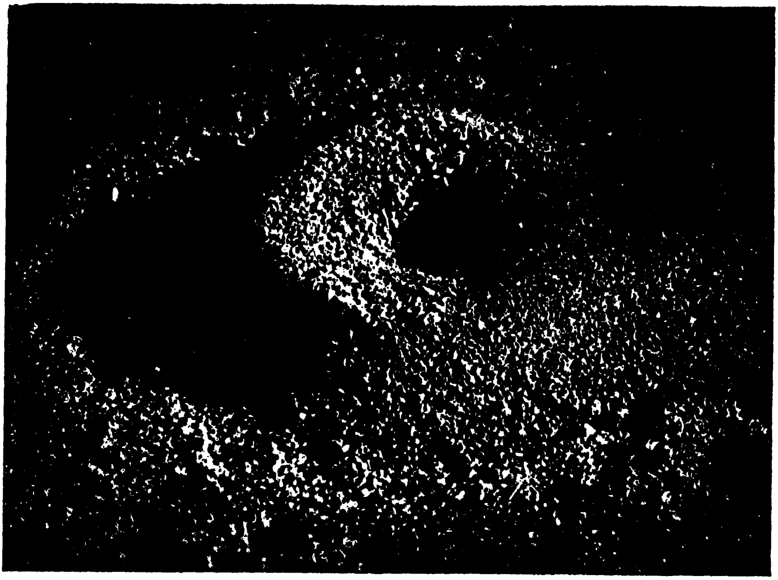


Fig. 45B

But when the ant has no desire to hide her nest, she fears neither large openings nor the deposit of the earthen pellets which she has dug out. Then there forms all round the nest what I have called a *crater* of earth, which serves the ants as a rampart. Craters of this sort are all very much like those depicted in fig. 45*A* and *B*, as constructed by *Pheidole Bergi* and *Conomyrma exsanguis*, which both live in the Argentine.

Fig. 46

In certain cases we find above excavated nests, instead of a crater consisting of loose pellets, a veritable rampart of earth-masonry in the form of a high tower, like that of *Trachymyrmex turrifex*, of Texas, represented in fig. 46. *Mœllerius Landolti* of Colombia, builds similar nests. In that of the Argentine *Conomyrna Wolfhügeli* the base of the crater, also of masonry, is narrow and then broadens out again like the calyx of a flower at the bottom of which lies the opening. This form is seen in fig. 47. In Colombia I myself have found magnificent calices artistically erected in very fine soil and surmounting the nest of *Pheidole praeusta*, and in that of *Elasmopheidole vallifica*, half-calices of a similar character forming a rampart on one side only.

Fig. 47

But the most curious thing of all is the central calyx of *Pheidole Sykesi* of India. It is surrounded by six or eight other ramparts, which all enclose it in so many circumvallations, the outermost being nearly a foot in diameter. I have in my possession a mould of this nest, whose sole opening is in the central calyx. The future alone can determine the purpose served by all these ramparts ; so far I have been unable to find it out.

Fig. 48

Besides single craters, certain ants such as our *Neomyrma rubida*, *Messor structor* and *Formica cinerea*, as well as *Messor arenarius* of the Sahara, have multiple or fused craters to one and the same formicary, made either of earth or sand. When they are fused, they form a gradual transition to masonry domes.

b NESTS WITH MASONED DOMES.—A large number of ants, especially in Central Europe, have a marvellous way of profiting by the rain when producing their earth-masonry. Domes of pure earth are then raised, which serve, as I have proved, to supply the brood with the warmth it needs. Some domes are regular, others irregular; some decidedly convex, others almost flat. Some are closed, others have one or many openings. Some, like those of *Lasius flavus*, are permanent, others like those of *Lasius niger* and several *Formica* and *Myrmica* species, are partly temporary, and some, such as those of *Tapinoma erraticum*, represented in fig. 48, are entirely temporary. *K* in this figure indicates the provisional dome; *Inn* shows the interior of the nest, which has no chambers or galleries, but consists solely of the stems and

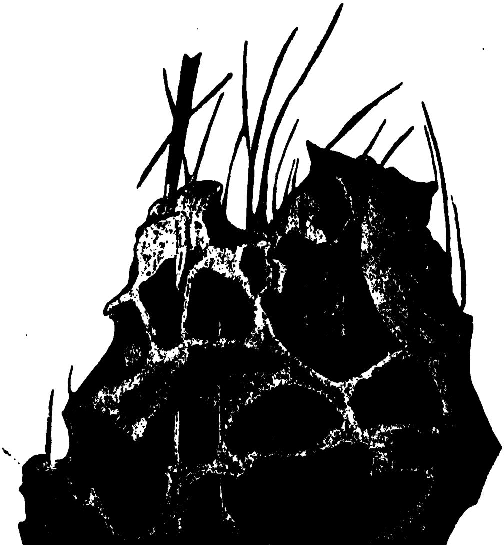


Fig. 49

leaves of green grass, passing through the dome, where the ants lurk with their brood; *Min* shows two galleries in the excavated (mined) nest, and *Er* the surrounding earth.

Fig. 49 illustrates how stems and leaves in the interior of a temporary secondary dome may serve as a support to the chambers and galleries which our *Lasius niger* carves out in her nest. We shall see in Volume III how she sets to work. The temporary domes rise up in the spring and dwindle and flatten in the autumn, until in winter nothing remains of the nest but what is permanent.

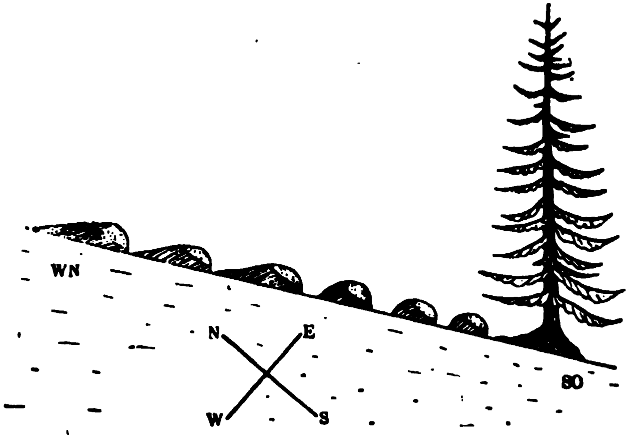


Fig. 50

Our *Lasius flavus* builds domes which are practically closed and almost permanent, but she needs them for her brood, although she lives in the earth and comes out very rarely. Huber, as early as 1810, and more especially Lindner at a later date, showed that on the slopes of the Swiss mountains the inhabited summit of her domes is regularly more tilted in the direction of the early morning sun, that is, from North-west to South-east, than in the opposite direction, as shown in fig. 50 (WN=North-west;

SO=South-east). Her aim in doing this is to get more warmth, and this again bears out my view as to the purpose of domes.

But if there were still any doubt about the matter, one well-established fact alone would be sufficient confirmation of my view; namely, that the domes are entirely absent in the east of the United States of America,

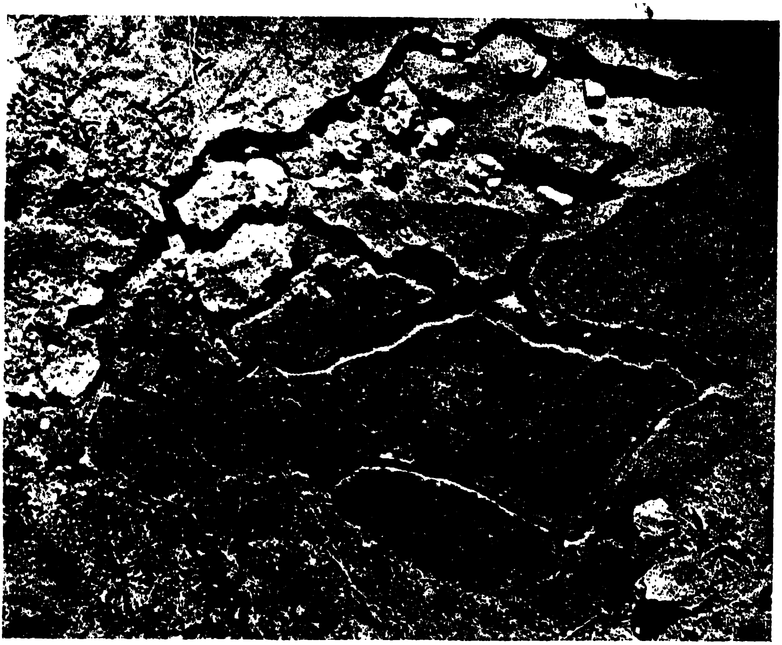


Fig. 51

whose climate is very warm in summer and cold in winter, except in the immediate surroundings of the Niagara Falls (whose spray falls back to the earth as fine rain)—even in the nests of species corresponding to those which build domes in Europe.

c NESTS UNDER STONES. Fig. 51 gives a fairly good idea of an ant-nest found under a flat stone which has been removed. Many ants, particularly in Central Europe, in the mountains, show a predilection for building their nests under stones which are more or less flat and medium-sized. In the Swiss Alps, for examples, at a height of 1,800-3,000 metres, scarcely any other sites than these are chosen by *Formica fusca*, *Tetramorium cæspitum* and the *Myrmica* species, as well as *Leptothorax acervorum* and *tuberum*, on barren spots or in short grass.

In this case the stone plays absolutely the same rôle as a masonry dome: it keeps the ant-brood warm and allows the warmth of the sun to reach them.

Directly underneath the stone, on the surface of the earth, we also find numerous large chambers and short passages tightly compressed one against the other and full of larvæ, nymphs and eggs (not shown, unfortunately, in our figure), as soon as we shift the stone. This is chiefly noticeable in the daytime and in fine weather, except when intense heat has the contrary effect of forcing the ants to carry their brood back to the bottom of the nest. In this region, the excavated chambers and galleries are more widely spaced; the interstices or walls, which seem so thin in the figure, are really much thicker. And for the same reason, in the deserts and tropics of the Eastern United States, we never or scarcely ever find ant-nests under stones; it is too warm for them there, and ants avoid the sun's rays.

2 NESTS IN SAND

Between sand and soil there are transitions of sandy soils, such as those in which *Formica cinerea* of Europe, for example, makes her nest. In the steppes, the soil is often sandy. In deserts and real sand-districts, masonry domes are therefore replaced by craters of movable sand-grains, like that in fig. 45 shown above, or somewhat similar.

In fig. 11 (Part I), we have depicted the long beards of the psammophores in the desert ants, and explained their function as 'sand-gatherers,' so well demonstrated and described by Santschi. In our coloured plate I, in connection with mimicry, may be seen beards like this, belonging to *Conomyrma exsanguis* and its imitator, *Dorymyrmex ensifer*. It is between the hairs of their beard, therefore, that ants endowed with psammophores hold the grains of sand which they extract from their excavated nest, in order to throw it out upon their crater. Those which have none, or an insufficient number—like *Messor arenarius*—are compelled to carry the largest pellets of sand in their mandibles when the sand is moist. This is seen in fig. 52, on the flattened, crescent-shaped crater built by this ant.

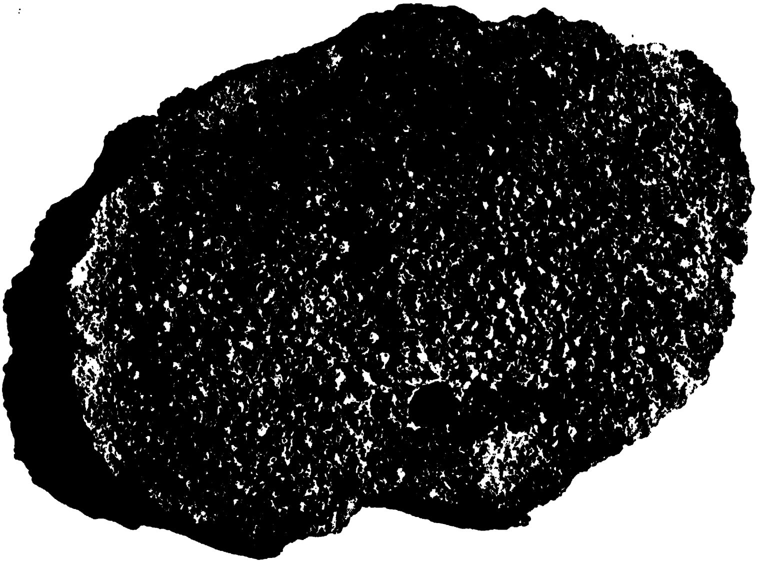


Fig. 52

These facts lead to the consideration of the depth and structure of certain excavated nests. In Switzerland, they

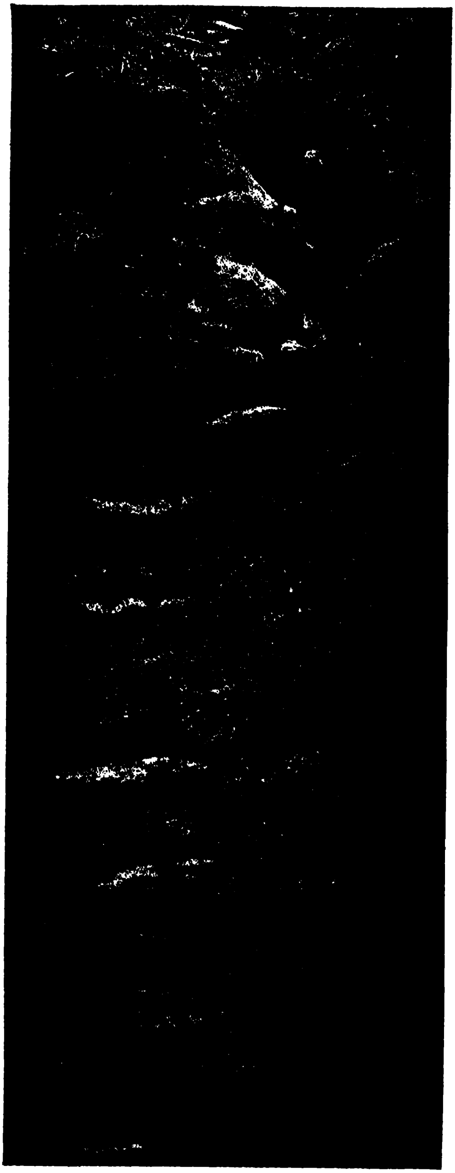


Fig. 53

rarely extend more than 30 or 40 centimetres below the surface of the ground, and the deeper and farther from the centre they go, the more widely the subterranean galleries are spaced. But in the steppes and deserts, it is different. While in Algeria, I was anxious to ascertain the depth of the *Messor arenarius* nest whose surface-crater is depicted in fig. 52. By digging a trench in the sand, I managed to connect two similar craters, situated 8 or 9 metres away from each other but forming part of the same nest. The canal leading to the bottom was oblique, so that after covering a distance of 5½ metres, and discovering one or two granaries, I had attained a depth of more than 1 metre 50 centimetres. There, after three and a half hours of work, with an assistant, I came upon a large granary with a second opening running upwards obliquely from its roof, in the opposite direction, towards another crater situated 9 metres away from the first. Thus a group of 6 or 7 craters situated 3-10 metres away from each other formed a single nest and a single formicary with granaries as large as they were distant from one another. It is probable that the nest extended still farther into the sand, under a surface measuring 50-100 sq. metres.

Whether it be in soil or in sand, for building granaries or fungus-gardens (see Part V) or some other purpose, certain *Myrmicinæ* build nests similar to that of *Pheidole Bergi*, represented in fig. 53 at half its natural size, after the excellent original photograph taken and reproduced by M. Carlos Bruch at La Plata. The crater of a similar nest has been reproduced in fig. 45 *A* at $\frac{1}{4}$ or $\frac{1}{5}$ of its natural size, but Bruch tells us that the nests do not all possess craters. Nests of this kind may reach a depth of 40-60 centimetres. From their single orifice downwards, they consist of a more or less vertical but sometimes spiral passage, with 5-10 lateral superimposed chambers, each 4 or 5 centimetres wide. All these chambers are connected with one another by the vertical canal. Now we are informed by the highly conscientious Bruch that *Pheidole Bergi* is not in the least granivorous, but feeds exclusively on insects. Moreover, its craters consist of very fine particles of soil, whereas those of *Conomyrma exsanguis* (see fig. 45 *B* above) are made of sand.

I myself have observed the very similar little nests built by *Oxyöpomyrmex Krüperi*; I discovered them in Salonica and afterwards described them. But this ant is granivorous and makes its granaries in lateral chambers superimposed upon one another round the central passage. It is chiefly to

Santschi that we owe an excellent study of the sand-nest of *Oxyopomyrmex*, which will be represented in fig. 112 (Part V). This nest has a sand crater 2½-3 centimetres high, built on a little diameter of 4-5 centimetres. Its funnel-shaped crater leads to the opening of a central passage 1-2 millimetres in diameter. The superimposed lateral chambers, three or four in number, all tend in the same direction; the lower ones contain the granaries.

At Kairouam, in Tunis, Santschi pointed out to me the tiny nests of the minute *Leptothorax Lauræ*, which are of absolutely the same pale colour as the sand. It is difficult to discern these diminutive craters, and the scarce-visible openings of the nest. This is a splendid example of sand-mimicry on the part of the ant which lives there.

Another interesting case was observed by myself at Salonica. Near this town, side by side with the numerous craters of *Messor structor* and *barbarus* r. *meridionalis*, built of dark-coloured soil, I saw some other light-grey craters of clayey soil in the midst of, but contrasting with the rest, on the same rich meadow-land. In these nests there lived a variety of *Messor Œrtzeni*, which is longer in shape than *structor* and *barbarus;* at a distance it resembles *M. arenarius*. I had no time to dig down to the bottom of the nests; but as the phenomenon was both obvious and of constant occurrence I concluded that the *Œrtzeni* nest is hollowed out to a much greater depth than that of *barbarus*, etc., that its passage passes right through the layer of humus and that its granaries are built in the deep-lying clay. The *barbarus* granaries etc. can be found as soon as we reach a depth of ½-1 metre.

Finally, certain *Pogonomyrmex*, especially the Mexican *barbatus*, cover the surfaces of their nests with small, black stones, while other species are content to lay this surface bare. Other *Pogonomyrmex* build enormous domes, and others again form craters.

3 SCULPTURED NESTS

The large ☿ of *Camponotus* properly so-called, *herculeanus*, with its races, *vagus* and *fallax*, in Europe and Asia; the varieties of those species; *C. pennsylvanicus*, *lævigatus*, *castaneus*, etc., in the United States; and different *Myrmamblys* and *Colobopsis* in various countries, all use their strong teeth and thick mandibles for gnawing through the wood of even the largest trees; they effect an entry through a flaw in the bark, which becomes their entrance-door. So that one fine day when a storm overthrows a large tree, we find its trunk pierced through and through with the galleries and chambers of ants, which spare nothing but the bark and the vital part. Fig. 54 represents such a tree-trunk, more than 40 centimetres in diameter. The photograph was wrongly printed, and should have been the other way round.

Near the bottom, nevertheless, we can distinctly see the door through which the ants go in and out. My readers should now picture to themselves how the other side of the trunk is riddled near the top with meandering furrows similar to those shown in the centre of fig. 13, but running on the whole longitudinally from

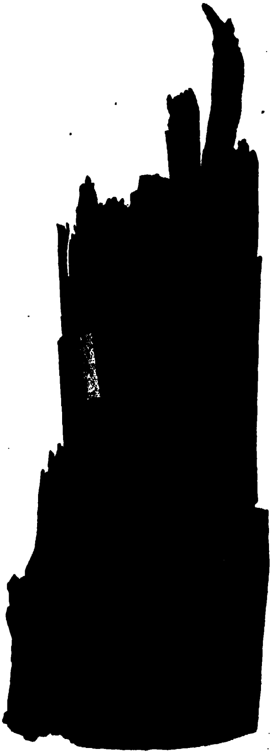


Fig. 54

the bottom to the top (the chambers being higher and the transverse walls shorter). They will then see in imagination and on a small scale what is in reality and on a large scale the trunk of a chestnut-tree, which was once sculptured by *Camponotus ligniperdus* at Vufflens-le-Château, and broken during a storm. This trunk was still full of ants when I had it sawn through. The wood properly so-called had been gnawed through and through to the centre, just as much as the sap-wood.

But these same ants very often also attack the beams of houses, châlets, bridges, etc., and frequently cause them to collapse. My advice has sometimes been asked on such occasions. When they can find neither a tree nor a beam, they nest in the ground. Frequently also they pierce the roots of their tree. The nests of *C. fallax* have fewer chambers, and their interior spaces have rather the effect of circumscribing the various layers of the tree than of forming labyrinths like those described above.

Certain species of ants also sculpture the exterior of the bark of trees. In this connection I would mention in particular many of our *Leptothorax*, among others *acervorum* and *corticalis*. In Algeria *Cremastogaster scutellaris* and its satellite, *Camponotus* (*Orthonotomyrmex*) *lateralis*, live in the bark of cork-oaks, without interfering in the least with their vegetation, but by perforating the cork itself. In fact, the ants which sculpture bark only sculpture its dead, dried portion; they never attack the *liber* or green, living portion which nourishes the tree and conducts the sap. Otherwise they would kill the tree which shelters them and enables them to live. We must be very careful not to confuse the ants which sculpture bark with those which are often found *under* the bark of dead trees. These, like a host of other insects, are merely utilizing the space left by the liber, which has decomposed and become friable after the death of the tree; these generally belong to other species—those of *Lasius*, *Formica*, *Myrmica*, etc., and we will say a word about them.

4 NESTS IN OLD TRUNKS, UNDER BARK, ETC.

In all damp countries, more particularly in virgin forests, but even in our more or less cultivated European woods, felled tree-trunks, the under-side of their dead bark, the moss surrounding them, the dry-rot and dried leaves which fill their more or less decayed empty spaces, serve as homes and as food for a host of insects, and many ants also make their nests there; these nests are extremely various, and nearly all belong to species which also dwell in the ground, our *Lasius*, *Formica*, *Myrmica*, etc. The worm-eaten wood and the rot of the trunks in decomposition are then partially substituted for the soil.

In this connection, our *Lasius brunneus* of Europe occupies a place apart. It lives in rotten wood, under bark, etc. and builds its chambers and galleries with worm-eaten matter. With this it also builds galleries in the clefts of the bark of living trees, wherein to milk its aphids; in a word, it constructs its normal masonry out of rotten wood.

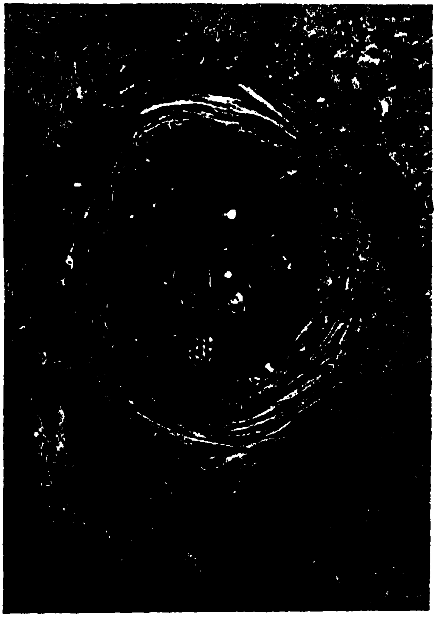


Fig. 55

Fig. 55 gives a good example of an incipient *Camponotus pennsylvanicus* nest situated under the bark of a tree. *Camponotus vagus* and our *Lasius affinis* often employ sawdust and wood-rot in a manner analogous to that of *Lasius brunneus*. Our *Myrmica ruginodis* and *Leptothorax muscorum* have a special preference for building their nests in moss, and the first is also partial to building on or in damp and rotten trunks.

In the virgin forest of Colombia I have often found *Pheidole* and *Stenomyrmex* in rotten trunks; among the firewood of a Colombian boat, I also discovered, stealing out from the underside of the bark, *Azteca polymorpha*, whose ♀ and large ☿ have very flat heads. In the same tropical country I took *Pseudomyrma Künckeli* in a dried branch whose labyrinth seemed to have been sculptured by her.

Most of the *Cryptocerini* are found in tropical American trees, especially on dead or sickly trees; I have myself found several in Colombia, *C. silvæ* among others. The problem is to find out whether they themselves sculpture this wood or whether they simply utilize the sculpture of certain beetles, or again, whether both these means are adopted according to the species.

In Switzerland, the ants which vary their materials—chiefly *F. truncicola*, but also *F. pratensis* and *sanguinea*, very often utilize felled tree-trunks as the base and starting-point of their nest.

Finally, in our marshes and peat bogs, *Lasius flavus*, *Formica picea*, *Myrmica*, etc., lean their nest, whether with or without masonry, against the tufts of moss and various plants, to prevent them from being damped or swamped; I have had occasion to observe this in Camargue, near Marseilles, among other places, and in the peat-bogs near Yvorne.

5 CARTON NESTS

Ant-nests made of carton are exceptional in Europe, but they abound in the tropics, especially those of America, Madagascar and India, and even in the virgin forests of Africa. They are found to an equal extent in the interior of trunks or branches, either hollowed by their workmanship or natural, that is, hollow originally, and on them—or even resting against the side of a trunk. Figures 56, 57, 58, 59, 60, 61, 62, and 63, as well as Plates V and VI, represent different forms of these carton nests.

Most probably the ants produce their carton in some fashion similar to that adopted by wasps, which also make carton nests, namely, with the secretion of their mandibular glands. These glands are highly developed in our *Lasius fuliginosus* and probably also in the other ants which make carton nests, and which are generally more or less swollen; however, we are still in need of serious study on this subject. Such secretions, which are also found in bees, may develop and become resinous in air, like that of the anal glands of *Tapinoma*, when they will often have a '*Tapinoma* odour,' and may form an excellent cement. This substance glues solidly together the particles of dry-rot, various fibres and other fragments of vegetable matter, or sometimes even earthen or sandy matter, which constitute the carton.

We will begin with *Dendrolasius fuliginosus*. It usually inhabits those trunks of our large European trees—oaks, walnuts, poplars, firs, willows, etc.—which have become hollow in the middle through internal rot. I possess a nest like this which is about 70 centimetres high and more than 25 broad. It was taken intact from the hollow trunk of an old poplar near Morges, by Warnery, who made me a present of it. The carton of these nests is made of very fine wood-rot. It is fairly solid, and nearly always covered by a fungus of velvety black, *Leptosporium myrmecophilum*, which gives it the colour of its ill-smelling ant. This fungus is found nowhere else, and therefore lives in symbiosis with *Dendrolasius*, for some purpose which has not yet been made clear. I have only seen one exception in a large fir-tree near Zurich. In this case, the whole nest was of a very light yellow, which enabled one to distinguish at a glance between its carton and the natural wood. In the ordinary black nests, on the contrary, the velvety black of the fungus covers both. This deceived Huber and caused him to believe at one time that *D. fuliginosus* sculptured wood and made its nest inside.

But this ant has other humorous tricks. If there are no trees at hand, she sometimes amuses herself by making her carton with the dry-rot in old houses, either between two boards or between two walls, or else under a beam. She then multiplies to such an extent that the owner is scared away. I saved one prospective victim by my expert advice, demanding as the price of my consultation that he should present me with the nest, which he gladly agreed to do. This flat, semi-circular nest, which is velvety black like the rest and situated between two boards, is 5 centimetres thick, 25 wide in its broadest part, and 50 long.

Finally, when she cannot find either a tree or any wood, our *Dendrolasius* builds dark-coloured carton out of sand. She glues the sand-grains firmly together with the saliva of her gland, and even puts small stones into the mixture. These nests are then as strong as they are heavy, but covered with the same velvety fungus as the others. When burnt with the blow-pipe they give out a few empyreumatic fumes and turn brick-red and more friable than they were before; but they remain whole, whereas the others are consumed, leaving nothing but a little ash.

All my efforts to see *Dendrolasius fuliginosus* construct her

Fig. 56

Fig. 57

carton under my eyes in artificial apparatus have been in vain, and others have hitherto succeeded no better; I have not depicted her nest, as it is well known and has no special peculiarity, except a labyrinth of chambers.

Fig. 56 represents the nest of the little *Azteca chartifex* r. *multinida*, which I myself plucked from a live branch in Colombia by standing up on my donkey's back—thereby causing myself a tumble. On various branches of the same tree there were a number of similar nests, constituting a polycalic colony. One of these nests is 11 centimetres long and 6 wide.

Fig. 57 shows the charming little carton nest of *Camponotus Goeldii*, perched on a bamboo. It is only 12 centimetres long, but has abundant succursals also represented on the twigs. It is obvious that in this case the ants glue together woody fibrils in strong preference to rotten wood. The figure is as eloquent as the nest itself, which Göldi sent me from Brazil.

Fig. 58 shows the main branch of a tree in the virgin forest flooded by the Rio-Purus, a tributary of the Amazon, bearing the enormous nest of *Azteca barbifex*, gathered and photographed by Göldi. The carton filaments of this nest hang down like stalactites, or rather like an enormous beard. The *Azteca* which builds it is only 2·5 to 3·8 millimetres long. By the same Rio-Purus, Göldi likewise found and photographed the nest of *Azteca Mathildæ*, which is 60 centimetres long and is represented in fig. 59. It is much

Fig. 58

simpler than the preceding example, and has round festoons covering its surface, as other species have. *A. Mathildæ* is a little larger than *A. barbifex*, in contradistinction to the smaller dimensions of its nest.

Fig. 59

Fig. 60 represents the hollow trunk of an oak filled by the carton nest of our European *Liometopum microcephalum*. This carton is more solid than that of *Dendrolasius*, and reddish in colour. At Æthos in Bulgaria I found this ant coming out of some enormous oaks, which were still standing and appeared to be sound and strong. But they must certainly have been hollow inside, like the one in our figure. On the other hand, the carton nest of *Azteca Mülleri*, represented in fig. 61, is found in the natural internodal (between the nodes) cavity of a *Cecropia adenopus*. This Brazilian tree is always hollow in the middle, from the very beginning.

Fig. 60

In fig. 62B will be seen the carton nest of *Tetramorium aculeatum*, set between a twig and a leaf. It was brought from the Congo by Kohl. Near the bottom are two entrance-doors, leading to its chambers. But most charming of all is the incipient nest of this ant, built by its ♀, which also appears at its natural size in fig. 62A. It is round in shape, attached to a single leaf, made of a single brown carton chamber and possessed of a single lateral opening. It shelters the queen-mother and her brood. In Trinidad, the adult *Camponotus* (*Myrmosphincta*) *folicola* makes a solid little carton nest, also consisting of a single chamber and opening by a single door.

Fig. 61

Next give a glance to fig. 63, which represents the grey, light carton nest of *Myrmicaria arachnoides*, somewhat smaller than its natural size and attached to a leaf with parallel veins. It was found by Jacobson at Wonosobo in

Java, at a height of nearly 800 metres. This nest, which measures 16 centimetres in length and 3 in width and height, is depicted twice, once as seen from above and on its leaf, the second time detached from it and seen from beneath. In this second figure you will admire the comparative regularity of the large chambers dividing up the interior of the nest, which is separated into two halves by means of a central partition, between the leaf and the slightly raised carton. The nest has no other orifice.

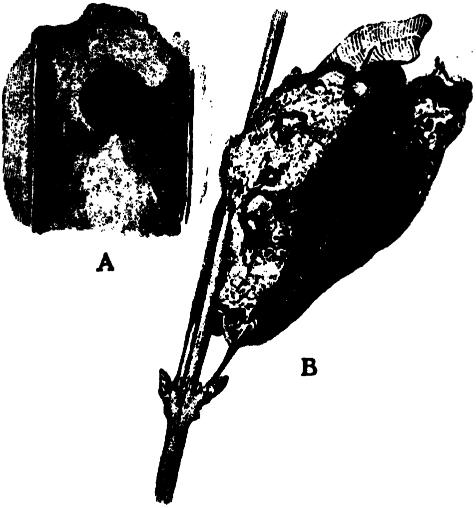


Fig. 62

Finally, Plates V and VI will show you in miniature two large nests belonging to two closely-related species of *Oxygyna*, a sub-genus of *Cremastogaster*. They are both from Madagascar. The one belonging to *O. Emmæ*, which I dedicated to my wife, is peppered with little holes for openings. By the side of it is the hand of a Hova, leaning against the trunk of the tree, and this enables us to judge

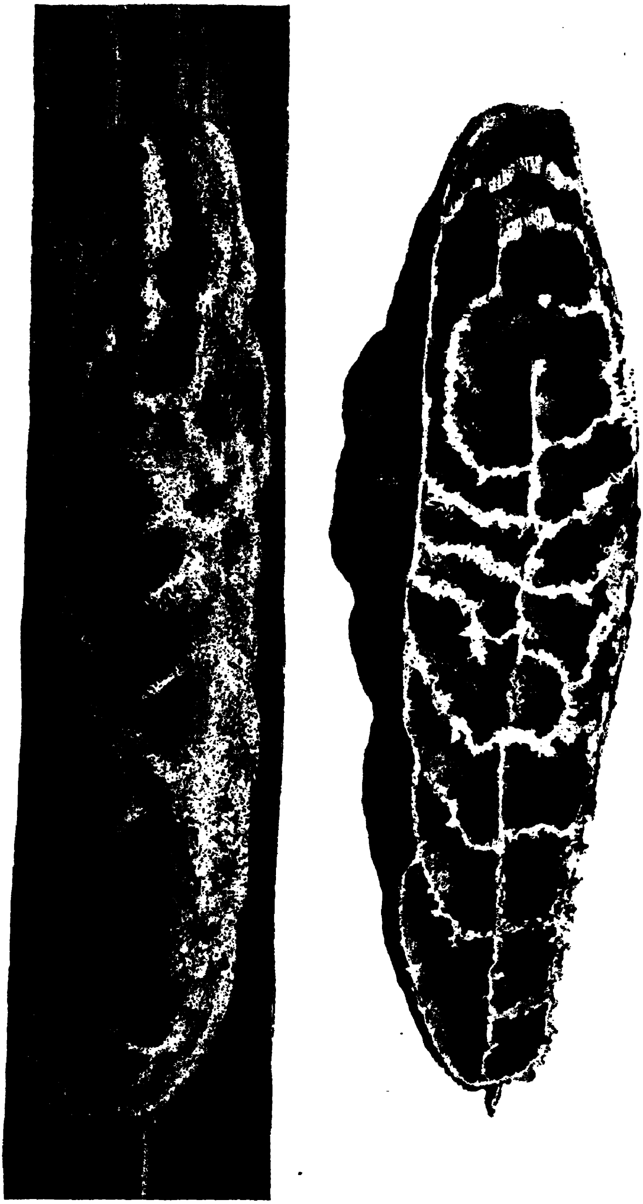


Fig. 63

of the real dimensions of the nest, which is about 50 centimetres long. The other nest, shown in Plate VI and dedicated to Ranavalona, a former queen of Madagascar, is situated between several branches and has a totally different appearance. It is about 30 centimetres in diameter. The interior of the nest has little chambers, closely compressed like those of the other, but as we come to the outer layers we find more and more of a much looser felt-like substance, consisting of long bundles of ligneous fibres, yellowish-grey in colour, interlacing with one another in all directions. Between these bundles lie meshes or intervals which grow larger as we get near the surface of the nest. The almost hairy appearance of this surface, giving, as a whole, the impression of being closed, can be seen very clearly in our figure, and contrasts with that of the nest belonging to the neighbour-species, *O. Emmæ*. The two ants themselves are between 3 and 4 millimetres long.

I hope that all this has given the reader a general and tangible notion of the carton industry among our little friends, and that it has also given them a desire to go to the tropics and study for themselves how these extremely various cartons are made; I should never come to an end if I tried to describe them all. In 1867 and later I sometimes saw the European *Cremastogaster scutellaris* build nests out of carton. Donisthorpe, Wasmann and Brun have even seen *Lasius emarginatus* and *umbratus* do the same.

6 WOVEN NESTS

The art of the weaving ants, *Œcophylla*, *Polyrhachis*, various *Camponotus*, etc., will be described and illustrated in Part V. Here I merely wish to give a short sketch of the appearance of the nests they weave by means of the thread of their own larvæ, which serve them as shuttles. These nests may be woven simply between the leaves, loosely

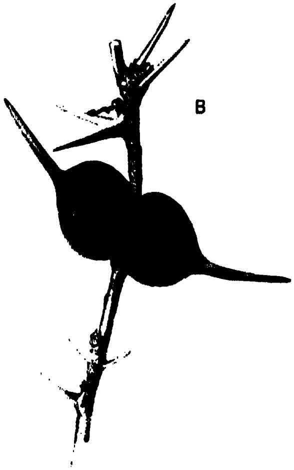
a. Nest of *Pseudomyrma spinicola* in an acacia spine. Tropical America.

b. Nest of *Cremastogaster Chiarinii* in spine of *Acacia fistula*. Tropical Africa.

c. Nest of *Procryptocerus spiniperdus* in spine of *Eurythrina umbrosa*. Trinidad.

d. Nest of *Pseudomyrma symbiotica* in a hollow Triplaris branch. Colombia.

H



B

D

C

E.W. [illegible]

connected with each other by a fine but firm fabric, or wide-meshed like a spider's web, as those of *Polyrhachis bicolor* are; or they may form an artistic imitation of a masonry nest or carton nest, containing countless chambers sustained by small silken pillars, and connected with one another by openings, as in the case of *Camponotus senex* var. *textor*. There is nothing, however, to prevent this last kind from being attached to a tree among the leaves surrounding a twig. Thanks to my friend, Dr. Goeldi, I possess such a nest, which is a perfect marvel, and also enfolds in its interior the nest of a little tropical bee of the genus *Melipona*. But the woven nests can also be made of a single sac of *close-woven* tissue buried in the ground, like that of the Indian *Polyrhachis simplex*, or again may be attached to a leaf with or without the intercalation of plant-débris more or less closely compacted.

When this plant-débris is really firm, the nest changes in appearance and seems at first to be made of carton. But its flexibility, together with its tenacity, show plainly that it is woven. In Batavia, Jacobson has found the woven nest of *Polyrhachis pressa* on trees covered with lichens. This nest, a tissue of bark, vegetable fibre, the hairs of certain seeds, little bird-feathers, etc., is woven so closely and afterwards so well covered up by the lichen that it cannot be distinguished from the tree between whose two forked branches it is fixed. It forms only one large, flat apartment, upheld by woven pillars, and has only one opening. I have in my collection a specimen of this fine example of mimicry between a tree, a lichen and a woven ant-nest.

Jacobson has made an admirable study of *Polyrhachis dives* and her nest. On the ground, woven between the grass-stems, he found the principal nest, measuring 24 centimetres in length, 10½ in breadth and 17 in height. So much dried débris of herbs, wood-bark, etc., was woven into its fabric that their brownish tint obscured the original weft. The nests of *P. dives* have numerous chambers. On the bushes round about stood these accessory nests or succursals, woven in the same way. Finally, Jacobson discovered the curious nests of *Polyrhachis Zopyrus*, which form a somewhat contorted tube, about as thick as a large pencil, rising 10 centimetres above the ground and composed of blades of the Javanese Alang-Alang grass in coils. Probably the weft had been spun, but it could not possibly be distinguished, even when the nest was broken. The opening is at the top of a tube, which is more or less vertical, but the nest extends underground. Whether the weaving of this nest is very weak, or whether the ants bind together the blades of grass with a little carton-saliva, we cannot decide without further observations. Many *Polyrhachis* nests, woven on or under leaves, have but a single chamber and a single opening, like the little carton nests of *Camponotus folicola* mentioned above.

7 NESTS FORMED IN PRE-EXISTING CAVITIES

The galls of certain insects, particularly those of *Cynips*, the spines of acacia-trees, the naturally hollowed stems of certain trees like *Triplaris*, the American *Cecropia*, the bulbs of *Myrmecodia* and *Hydnophytum*, the hollow dry stems of brushwood and the twigs of trees in general, those of reeds and Graminaceæ (grasses)—in short, all hiding-places or natural or artificial cavities may be used by the ants as nests.

Plate IV *b*, shows the typical spine of an African acacia, gathered by Prof. C. Keller in Somaliland, and containing a nest of *Cremastogaster Chiarinii*. This spine, which we have already mentioned in Chapter III, is swollen at the base and pierced with a hole, like all spines inhabited by ants, and like the one represented in figure *a* of the same plate. This last, which is all swollen, is inhabited in Costa Rica by

Pseudomyrma spinicola. Sjöstedt thinks that the swellings are due to Coccids or gall-insects, which, in Africa at any rate, cause certain spines to swell in this way and form galls. It is thought that the ants pierce the opening themselves.

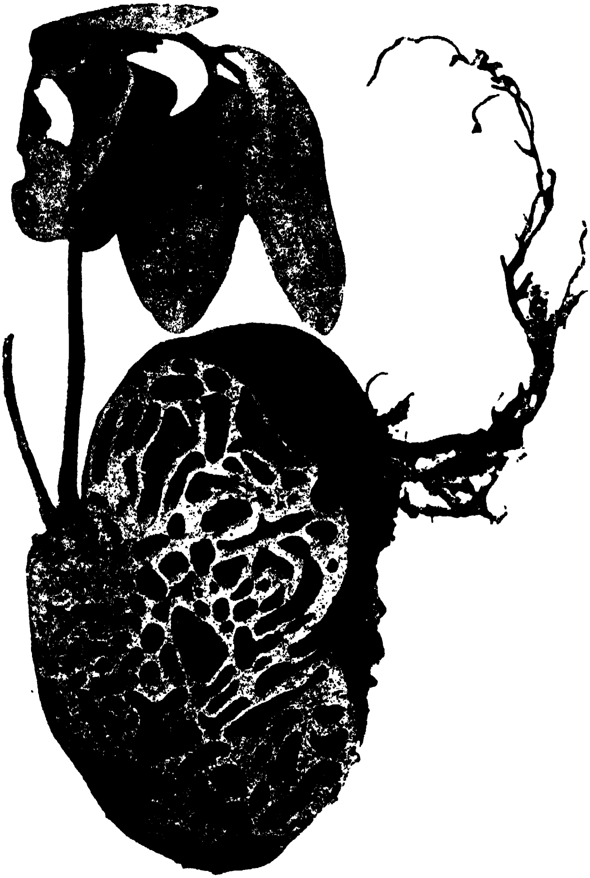


Fig. 64

The shape and length of these structures varies a great deal. Sometimes, as we said before, the ants construct a few chambers in their spine.

Furthermore, various spines have bases of solid wood, like ebony. Certain ants, however, such as *Procryptocerus spiniperdus* of Trinidad, already mentioned above, choose these sites in which to sculpture nests such as we illustrate in Plate VII *c*.

Fig. 65

Various plants have *phyllomes*, that is, special cavities in their leaves, often inhabited by ants. This is the case, for example, which the plants known as *Tococa*, *Duroia*, *Maieta*, etc.

In connection with symbiosis between ants and plants, we have already mentioned the natural cavities of *Triplaris*, shown in Plate VII *d*, which shelter *Pseudomyrma symbiotica*. It is the same with the primary, natural labyrinths in the tubercles possessed by *Myrmecodia* and *Hydnophytum*, represented in fig. 64, and already mentioned above.

Fig. 65 shows the nest of *Camponotus* (*Colobopsis*) *etiolata*, of the United States, hollowed out in an oak-gall, with the ☿ and ♃ ants themselves inside the gall.

But it is much more usual, both in the tropics and in Europe, to find the stems and branches which are dead, dry and hollow, occupied by a host of ants, intent on dwelling there without any further construction, either of carton, earth or tissue. In 1896 I was wandering about a Colombian savannah, searching in vain for the nests of various ants. Despite myself, I sat down near a tuft of grass and said—laughing at the idea : "Could ants, by any chance, live in dry grass-stems ?" Thereupon I began to break some stems of this sort, without even getting up. No sooner had I snapped the third stem than out ran a host of *Pseudomyrma gracilis* with larvæ and nymphs, and others followed from the next stems. Then the scales fell from my eyes. It was midday. In the afternoon I went back to the brushwood, laden with tubes of alcohol, and began to break the dry, hollow stems of all the bushes I found. Never in my life did I have such a phenomenal harvest of ants, ☿, ♀, ♃, ♂ and brood, in the space of three or four hours. To expedite matters I began simply to blow into one end of the broken stem from which the ants were pouring out, in order to make them fall straight into a tube of alcohol which I held in my hand. Thus in this very short time I discovered the hitherto unknown winged sexes of several species, and even some new species. Next day, unfortunately, an accident occurred, and my return to Europe prevented me from confirming what I had found out until I could put it to the test in

Jamaica and St. Lucia, and later on in Switzerland, among the dry branches of our walnut-trees.

In these particular trees, we find fairly regularly the polycalic colonies of *Colobopsis truncata* and *Hypoclinea quadripunctata*, as well as the simple formicaries of *Leptothorax affinis*, as I was able to ascertain in the Canton of Vaud, but not until my return from Colombia. Some time afterwards, Dr. Stäger found various *Leptothorax* nests in Valais, in the dry, hollow stems of *Rubus ulmifolius*. I myself had previously found some in fallen stems scattered about in dry places, without at the time considering the general significance of the fact. Finally, near Smyrna, I discovered a number of *Camponotus lateralis* in some dried reed-stems. On the whole, therefore, this phenomenon seems to be very general in warm countries, and in Europe in those dry places which are described as xerothermic.

Fig. 66, already mentioned, represents the symbiotic nest of *Camponotus quadriceps*, built in the stem of the Papuan *Endospermum formicarum*, with its light and porous pith. It has 'extra-floral nectaries,' and an ant is seen tasting this 'nectar outside the flowers' at the base of a leaf.

8 NESTS OF NOMADS AND OCCASIONAL NESTS

By *nests of nomads* I mean those of the *Dorylinæ*, which are nomad and transfer their habitat from one place to another during the night, with all their brood. These ants will scarcely take the trouble to construct nests for themselves, for their hunting-expeditions compel them to emigrate at any moment. When they are not stealing, for the time being, the nests of other ants or termites which they have slaughtered, they are content to find shelter in a hollow tree, or a decayed trunk, or the sand, in some fashion which I do not as yet clearly understand, but always without doing any proper building themselves; sometimes they actually live in

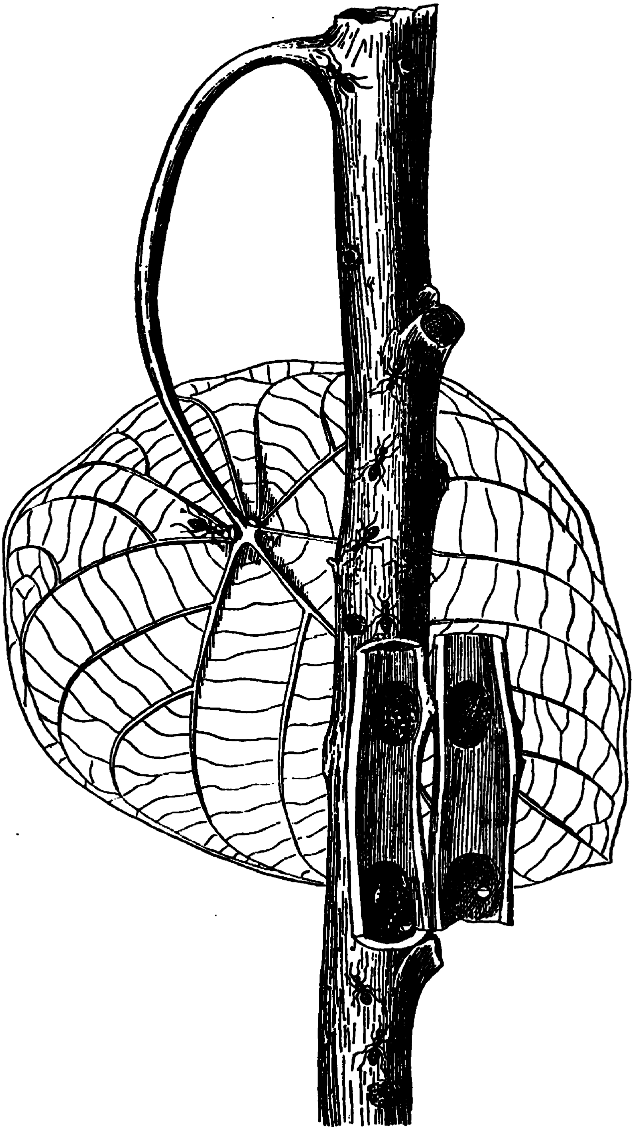


Fig. 66

the open air, where they link themselves together by their long hooked mandibles and form great ant-balls. The brood and the small ☿ are then enclosed inside the ball. The same thing happens in districts which are temporarily flooded. The *Dorylinæ* adopt this means of preserving their brood from the water, and allow the current to drift their communal ball to some piece of ground from which the waters have provisionally receded. Under the same circumstances other kinds of ants resort to similar measures.

The same *Dorylinæ* can throw across a stream real living bridges consisting of ants linked one to another; the whole band then passes across this bridge. In other places, they build tunnels through sand or soil for a like purpose (*Eciton prædator*).

Once only have I found, in the dry-rot of a decaying tree in North Carolina, the provisional nest of *Eciton carolinense*. The trunk was literally impregnated with *Eciton*, nearly a foot above and a foot underneath the ground. Not an inch of rotten wood was exempt. I cut the whole thing down to the ground with my chisel, laying bare the roots in order to discover the ♀; and in the end I found her.

The nests built by *Acromyrmex octospinosus* in the open air among the grass or bushes might be described as *free nests*. They consist simply of mushroom-gardens; we shall discuss them in Part V.

By *occasional nests* I mean those which shelter our *Lasius emarginatus* in the insterstices of the foundation-stones of our houses, so that they do not have to build anything. *Cremastogaster scutellaris* in Ticino sometimes does the same thing between the stones of walls, and so do the cosmopolitan *Prenolepis longicornis* and *Iridomyrmex humilis*. The interstices alone constitute the nest. Under this heading we can also place the accidental nests of certain ants; for example, that which *Camponotus* (*Myrmoturba*) *stercorarius* usually constructs in Guatemala, by excavating and building chambers in dried cow-dung.

9 NESTS IN ROCKS.

In Europe, it is chiefly *Aphænogaster subterranea* which inhabits the interstices of rocks, and despite the epithet 'subterranean' scarcely ever constructs nests in the ground. Various *Leptothorax* and *Lasius emarginatus* often do the same. In 1909 I discovered at El Kantara in Algeria, in two places, a species which was then new, the big *Aphænogaster rupestris*. One nest was situated in a cleft in the rock, the other in a wall of strong masonry, from which the ants came out through a hole bored in the cement.

Fig. 67

10 VARIOUS COMPOSITE NESTS

The typical composite nest, seen in figure 67, is that of *Formica rufa*, *pratensis*, *truncicola*, *exsecta*, *pressilabris*, *picea* and *sanguinea*, and also that of the corresponding species in the United States. But according to the species, the dome may be rounder, smaller, or flatter than that of *F. rufa* in our figure.

The top and middle of this dome are composed of mobile materials of all sorts; fir and pine needles, cut stems of grasses, the débris of leaves, fragments of resin, and even snail-shells or small stones. In this part of the nest, the ants intermingle the materials in question in such a manner as to construct a labyrinth of very irregular spaces, whose apertures they close in the evening and during rain, and open again in the morning or when the fine weather returns. This whole labyrinth rests on an earthen base of rough masonry. But the division between the tangled material and the masonry is indefinite, as the ants cover some of this material at the bottom of the nest with earth. Lower still, the masonry galleries become more and more widely spaced, as they do in the nests of pure earth. *F. sanguinea* uses very little movable material; her nest forms a transition to the pure masonry type. In that of *F. exsecta* and allied species thin straws and leaf débris predominate. But this is especially true of the *Serviformica picea* nest, which is made in our peat bogs out of the very fine débris (leaves and stems) of *Schœnus ferrugineus*.

Tetramorium cæspitum, *Lasius niger*, *Serviformica fusca*, *etc.*, sometimes also amass a certain amount of movable material at the top of their domes. In Western Australia, *Iridomyrmex conifer* makes her conical dome out of the husks or waste-product of seeds. The nests of *Polyrhachis Zopyrus*, to which reference was made above, are also composite nests.

Among the most curious composite nests, some mention must be made of those which are built by many species of

Polyrhachis, such as *P. Jacobsoni* in Java, *ceylonica* and *thrinax* in Ceylon, etc., which combine the fine fabric woven by the larvæ with the carton secreted by the mandibular glands of the ant herself. I myself have demonstrated this combination in small nests of various species, constructed on leaves, which were sent to me; the woven fabric is inside and the carton outside, the fabric only remaining on that part of the nest which is attached to the leaf.

We may also classify under this heading the ant-gardens built in tufts of epiphytes, of which we shall speak in the next Part.

II DOUBLE NESTS AND STOLEN NESTS

We have already used the term double or multiple nests when describing the cases in which enemy ants dwell under the same stone, or in chambers and galleries back to back with one another, or even intermingled under the same dome, built in or on the same tree or in the same hollow stem, separated only by partitions. This happens, for instance, in the case of *Solenopsis* and others which live in lestiobiosis (see Part IV) with large ants or termites. A curious case in point is that of the little *Formicoxenus*, which lives as a guest indifferently supported in polycalic colonies, with small multiple nests in one large *Formica rufa* nest, as Stumper recently proved.

From double nests, we pass to numerous cases in which ants steal nests from each other or from termites; and then goodbye to specific architecture. We can always recognize a nest stolen from termites, but much more rarely those stolen from another ant-species or genus, and then only by its architecture. Large ants increase the size of the chambers and openings of the nests they steal from the small ones, and *vice versa*. Among the victims, *Lasius flavus* is prominent—among the thieves, the *Dorylinæ*.

B Constructions Outside Nests

I SUBTERRANEAN PASSAGES AND FREE PATHS

All ants capable of excavating the earth can extend the subterranean part of their nest in the form of passages, and this enables them to search for aphids or for prey, or to escape in case of danger, or to come out of their nests without being seen. In Brazil, Bates noticed how some sulphur-fumes which had been put into an *Atta cephalotes* nest, with a view to destroying it, were coming out again 70 paces away from the nest. Our *Lasius flavus* and *Formica fusca* are very clever in this respect, and so are *Tetramorium*, *Solenopsis*, etc. The expeditions of *Polyergus rufescens*, reserved for Part IV, will bring us to the heart of the matter.

Other ants, on the contrary, file freely after each other under the ground, and nothing special can be perceived on their track, even when they always use the same path.

2 OPEN AND COVERED PATHS

It is quite otherwise with the regular and multiple paths which our European *Formica pratensis*, in particular, builds on the surface of a meadow in order to facilitate her traffic across the grass.

These paths are made, cleared and industriously kept in order by the ants, which even cut down the stems of grasses for this purpose, and continue digging until they have a hollow on the surface from two to five centimetres broad and from one to two deep. *F. rufa* and *Dendrolasius* also make open roads, but theirs are less distinct. Moreover, as they wind farther and farther away from the nest, whence they all originate, the hollowed paths become less and less distinct.

Still more interesting, however, are the covered roads which *Formica integra* of the United States, for instance, builds out of the same small, movable materials as those which compose its nest. This nest is similar to that of our

F. exsecta, etc., and the roads are made for the same purpose as those of our *F. pratensis*. These roads are hollowed, narrow and tortuous. The material of the vault which covers them is sometimes broken, and for a short distance the road is then uncovered. *Eciton prædator* of tropical America constructs similar roads in the soil along which to hunt her prey. And in Europe, *Lasius niger*, *alienus* and *brunneus* construct covered roads across footpaths, or even up walls, trees and bushes, to enable them either to travel from one nest to another or to go and milk their aphids. Fig. 89, Part III, will show them in the very act of building.

3 STATIONS, PAVILIONS AND SUCCURSALS

The three types of construction with which we are concerned here, whether open or covered, are more or less separate from the nest without being complete nests.

I use the word 'station' in reference to the shelters which ants hollow out on their paths, generally in the earth, in order to place themselves temporarily under cover. Our *Formica pratensis* and *Lasius niger* frequently carve out such refuges, which they utilize when the night, the rain or the cold comes unexpectedly upon them. It may consist of a simple chamber, or may be a very small partial nest.

I have adopted Huber's term 'pavilion' more especially for the masonry works inside which the ants sometimes enclose their aphids and coccids, both to protect and to milk them. In fig. 92, Part III, will be found a pavilion like this set up against the stem of a plant, as an adjunct to a *Lasius niger* nest. *L. emarginatus* will also sometimes produce one. Fig. 93 of the same Part, on the other hand, shows a pavilion entirely separated and at some distance from a nest of *Cremastogaster pilosa*, of the United States. Our *Myrmica* species sometimes have similar constructions.

Finally, I have christened 'succursals' certain small accessory nests which the ants make out of masonry, carton or woven fabric, according to their special art, and which may sometimes develop into the complete nests of a polycalic colony. Figure 57 is an excellent example of two small succursals made of carton, each on a twig of the bamboo to which the principal nest has been adapted. The figure is less than half the natural size, but the nest itself is small.

4 POLYCALIC COLONIES

As we said before, the double or triple nests contain several formicaries. Conversely, polycalic colonies are formicaries possessing several nests. The Germans use the term *colony* where I should use the term *formicary*, that is, for a social unit of ants, whose intimate mutual relations are friendly. To avoid all confusion, in this case I add the term 'polycalic' (with several nests) to that of colony or formicary. The largest polycalic colonies known are those of *Formica exsectoides* of the United States, among which McCook counted as many as 1,500 nests constituting a single formicary, connected by numerous files of friendly ants, and covering a vast stretch of ground. On Mont Tendre, in the Vaud Jura, I myself counted 200 similarly connected nests belonging to *Formica exsecta*, extending over a circular area with a radius of 150 to 200 metres.

As a rule, however, the number of nests in a polycalic colony is not above thirty, even in the case of *Formica exsectoides*, *exsecta* and *pressilabris*, all of which are hardly ever content with a single nest, except in the early stages of the formicary. The old formicaries of *Formica rufa*, *pratensis* and *truncicola* often have from two to four nests.

Raptiformica sanguinea very frequently has two nests, which she inhabits alterntively, one in summer and the other in winter, when she captures her slaves, as I had already proved in 1874, and as was afterwards confirmed by

Wasmann. But it is a very interesting fact that the American race *aserva*, which captures slaves only during the early stages of the formicary, lives regularly in polycalic colonies of twelve and more nests. On rare occasions, however, I have observed a polycalic colony of our European *sanguinea* consisting of some thirty or forty nests, without a single slave. Further observations are wanted; we must not generalize.

In Trinidad I found an enormous tree covered with *Dolichoderus bidens*. These ants seemed to be sheltering in little carton nests, each constructed under a leaf with an opening at the side, or else between two leaves linked together by the carton. The inhabitants of these countless nests were all in friendly communication. They themselves were from 6 to 9 millimetres long and had then no brood, or very little, in their small nests. I wondered whether there could be a central nest anywhere, but I did not find one. On the contrary, the carton nests of *Azteca multinida* in fig. 56 are true complete polycalic colonies. There are still many discoveries with regard to all this to be made in the virgin forests.

I would also here recall the polycalic colonies of *Formicoxenus nitidulus* in one and the same *Formica rufa* nest. It is almost certain that *Cremastogaster* and *Pseudomyrma*, which live in acacia-spines, *Azteca hypophylla* under its leaf, and the ants which inhabit the Tococa, Duroia, etc., also form polycalic colonies on their tree or bush.

The *Ponerinæ* and *Dorylinæ* never make nests of carton or woven tissue, or polycalic colonies—at any rate, so far as we know at present—and they are not very adept masons.

Here, then, we close Part II. We have dealt with a medley of subjects, sensations, physiology, psychology, symbiosis with plants, syndiacony, guests, parasites, poisons, monstrosities and nests. But it was essential to gain some clear idea about all these things, after the subjects discussed in Part I, so as to be in a better position to attack the problems of ant-habits, within doors and without, including their specialized habits. The next three Parts will be devoted to these three subjects.

The ways of the Creator are unfathomable—so said our fathers. Our reply is that the ways of nature can be fathomed perfectly well, with perseverance and toil, by the human brain. The things that are, and always will be, unfathomable are the pseudo-problems of metaphysics, with their divagations into an alleged unknowable 'Absolute' of the Universe. Let us learn, therefore, to be content with the relations between this self of ours, a function of our brain, and the external world surrounding us. Let us bow in resignation before the unfathomable essence of the world, and before the hypothetical First Cause of wickedness and ugliness, as before that of the goodness and beauty, which we may discover at every step if we search carefully about our little planet. Let us admit that the notions of good and bad, beautiful and ugly, are only relative to ourselves and our sensations. Let us imitate the ants of a single polycalic formicary; we shall then become more modest and sociable throughout the entire world by the federation of all peoples.

PART III

Part III

INTRODUCTION

Ants, being anarchists and communists at the same time, realize the ideals of both Proudhon and Kropotkine for human society, but they do so by means of a natural instinct inherited during the egg-stage, such as we have no claim whatever to possess. Owning neither government, rulers nor laws, they all usually inhabit the same nest and common chambers. They do not indulge in family apartments, separate workrooms, personal attendants, kitchens, dining-rooms or bedrooms; the whole of their internal and domestic life, both that of the young and that of the adults, is conducted in common. Intimacies and family secrets, which must not be divulged, are also rarely found among them—for nearly all their nuptials take place in the open air.

Their home life and its customs are therefore evolved by our little friends in the darkness of their common nest, and only occasionally at the surface, in the surrounding district or on roads which are also common property, for the ownership of land is socialized as completely as that of the means of production and consumption. Otherwise, what could be the significance of these means, among creatures whose individual bodies, even, have social stomachs incomparably larger than those which digest food for their precious selves? And you, friend reader—have you yourself thoroughly digested the above-mentioned consequences of communistic life among the ants ? If you wish to understand their habits, you must certainly do so.

But before we human egoists can make a thorough study of the home-life of ants, we must resort to a subterfuge in the shape of artificial apparatus, which can force them to reveal it to us. In a word, we get a whole community into our power in such a way that we can watch and observe it at leisure through a glass which allows light rays, visible to us, to pass through it. Our first chapter is, therefore, devoted to the description of the various forms of observation-apparatus which have hitherto been invented.

In our second chapter we shall follow the ants to their poetic aerial marriage-flights, wherein all enemy tribes, with one exception, are intermingled in love. There are no more formicaries in the upper air; each species only seeks its own kind, to unite in a nuptial embrace which is exempt from all jealousy. But after this we must also follow the fertile ♀ to their cenobite life, in which they act as the queen-mothers of formicaries.

The third chapter will show us life inside the nest, nutrition, hygiene, work, migrations, rest, and even ant-games of various kinds.

In a fourth chapter we shall pass on to the art of building and migration from one nest to another. Here we shall also see how the life of each individual is adapted to the social needs of a collective community.

We shall then describe, in our sixth chapter, the manner in which ants practise cattle-rearing, mainly to our disadvantage. Here we shall see not only the open-air system of rearing, but also various kinds of social byres, quite as good as our own.

After devoting a short sixth chapter to ant-gardens, we shall conclude with a seventh, giving an account of the history of ants which live as parasites upon other ants. These creatures are more in the nature of symphilic and synœketic guests, of which we spoke in Part II, Chapter IV, than of true parasites. But the guests in question are themselves communists. Two communisms, one of which exploits the other—the situation is not lacking in originality.

We shall thus adopt a method the reverse of Cæsar's, and prepare for the warfare of ants (Part IV) by a description of their peaceful collective life—prepare for war, in short, by peace. The reason why lasting peace is unfortunately impossible on this planet, so far as our little friends are concerned, has already been mentioned. Scarcely any of their colonies can exist without war, unless its members become the parasites or guests of another colony.

Chapter I

OBSERVATION APPARATUS. EXPEDITIONS

Gould, the author of *An Account of English Ants*, who quoted Pope's description of the anarchy of ants, well-organized without government, recognized as early as 1747, with much more perspicacity than his successors, that Solomon and Pliny might be right in attributing granaries to the ants of their own hot countries, though the English species are lethargic during the winter. But Gould had not as yet, to my knowledge, constructed artificial apparatus in order to observe ants. He studied their habits in the natural state.

1 Apparatus. So far as I know, Pierre Huber was the first to use contrivances of this sort. One apparatus used by him consisted of two vertical panes of glass set close together in a wooden frame and fixed under a table. When opened between the two panes, the table is covered by a glass bell-jar, underneath which the ants can construct their upper dome, while their doings and movements in their underground tunnels can be observed between the two panes.

In 1867 I thought it would be best to modify Huber's glass apparatus as follows: Two panes, 40 centimetres long and 31 centimetres high, were set and cemented into a wooden frame, at least 3 centimetres away from one another. In the middle, they were also separated by a sheet of tin. This sheet was perforated by a number of holes, only 3 millimetres in diameter, and 8 or 9 millimetres away from one another. Thus the large *Formica*, for which this apparatus was designed, have only 1½ centimetres at most in which to construct their chambers, and are compelled to lean them directly against the glass, since the holes in the tin allow them to pass, but not to build.

One of the narrow sides of the wooden frame, furnished with little hooks, is movable, and can be opened from bottom to top when it is necessary to clean the nest. In addition to this, two movable wooden shutters, covering the whole structure, make it possible to intercept the light, for the wooden frame of the apparatus is only 3 cm. wide inside. Lastly, that portion of the frame which can be opened, 8 cm. above the earth, is perforated with a hole 1 cm. across, allowing the insertion of a tin tube, to which a manger of thin iron or copper grating, about 10-12 cm. long by 6 cm. deep by 8 cm. wide, is connected by a rubber tube. A manger of this sort, which can be removed and put back at will, is utilized by the ants, both as a receptacle for the food which the experimenter provides and as a depository for their refuse. Finally, on top of the frame of the apparatus, held vertically upon its narrowest part, a small opening, closed by a cork, enables one to moisten the earth when necessary.

This apparatus is extremely portable. I have used it at various times to transport from Vaux to Zurich and *vice versa* my different colonies of *Polyergus rufescens* and *Formica sanguinea*, as well as a number of experimental mixed colonies, and have kept them there for many months.

I modified this apparatus to accommodate small ants by making it smaller, with a single tin frame, and two panes of glass scarcely 1 centimetre apart. In this case the frame, which is covered simply by a sheet of cardboard, must be placed flat on one of its big sides. The manger is the same. It retains moisture only too well, for a portion of it is often covered with mould. I have studied *Tapinoma erraticum*, for instance, in a nest of this sort.

The following conditions are preliminary to the use of all such apparatus. Arm yourself with a good small chisel with a very sharp edge, and use it as a lever, after burying it in the earth at one side of the ant-nest you wish to remove; this will enable you to lift it. For large nests a spade is sometimes required. But when you have removed the nest and its inhabitants, you will need to place it somewhere provisionally. In this connection an ant-bag, which may be large or small, but which must close securely and quickly, is indispensable.

And now that you are laden with the precious spoil you have so callously thieved from the poor inhabitants, which are all upside down and distracted, the problem is, how to get them into your apparatus. In this connection, I once hit on a very practical method. Before putting ants into an apparatus, provide yourself with some very fine powdered plaster of Paris, and, before pouring out your bagful of ants, make somewhere, with this powdery plaster, a circular arena fairly wide and fairly high, to serve as a wall. Put it into direct communication with the tin tube of your apparatus, after provisionally removing the manger and introducing into the apparatus a fair amount of earth, slightly (not overmuch) moistened, to enable the ants to construct their masonry nests here later on. Only then should you pour out the contents of your bag, either gradually or all at once, into the plaster arena, which has been kept very dry.

You will thus be able to observe, entirely at your ease, what the ants and their brood are doing. The moisture which they will perceive with their antennæ will entice them to the opening of the tube, that is, into the apparatus. There they will discover damp earth, and will hasten to migrate thither with their brood, especially if the shutters are closed. Furthermore, put a little honey or sugar into the arena for them. In this way you will be able to observe at your ease the art of building, migration and mutual regurgitation, and descry any guests that are present, etc., etc.

It is certainly simpler to unload the bag of ants directly into the tube of the apparatus. The man whose interest in the intimate habits of ants has already been surfeited, or who is short of time, will proceed in this way. Then everything happens in the dark, and your nest in the apparatus is soon an accomplished fact. To begin with, the ants wander all round and try to climb the wall of powdered plaster, but they only succeed in covering themselves so completely with dust that they soon grow disgusted. Here lies the secret of the success of the plaster arena. Hitherto I have seen but one ant, *Tetramorium cæspitum*, which is capable, after much perseverance, of crossing a plaster arena, and it does so by making minute perforations in it in a transverse direction. It succeeds—how I cannot say—in keeping these little passages open through the powdered plaster.

Plaster arenas, especially in the case of small ants which one may wish to study without transporting them elsewhere, can be used alone, instead of the glass apparatus, and serve the ants as a nest. All that is then required is to put into it a little damp earth, wood-rot, wood or bark, and lastly the necessary food. The most important thing, in this case, is careful attention.

When transporting a nest of ants in a bag to find them a new home in your apparatus, you should take care not to shake it, and should first put a leafy twig or a little damp wood into the bag, so that ants and brood may be injured as little as possible, and may cling to it or disengage themselves while still in the bag.

For experiments with only a small number of ants, it often suffices to utilize a simple vial closed at the top, with a little earth or wood at the bottom. If you attempt to enclose formicaries in a circular moat full of water you are liable to perpetual disappointments; the ants cross the canal or drown themselves in it.

Finally you must know how to manipulate ants without injuring them; I recommend the use of a pair of fine watchmaker's pincers, with which you should seize the ant, if possible, by one of her hind or middle legs, never by an antenna or by the body. Insects should sometimes be killed and added to the honey or sugar which you give them for food.

But since Huber's time and my own, great progress has been made in apparatus for rearing ant-colonies, and I must tell my readers about it.

Lubbock (1875-1880) constructed a glass apparatus similar to my little tin apparatus, with two plates likewise only 5-12 millimetres apart. But his frame is made of wood, the glass being set in it or fixed by small clamps. Usually only the lower pane of the nest, which is always horizontal, is cemented to the frame. On the other hand—and herein lies its great superiority over my primitive nest—the upper plate is mobile and may even be divided into three portions, each of which can be removed, replaced, cleaned and covered at will. The lower plate can be covered afresh with a variable amount of earth for the ants, according to circumstances. Lastly, one side can be connected by a tube to a manger or other accessory apparatus used for the ants' refuse or for other purposes. The interstices which might provide a passage for very small ants are filled with wadding. Finally, Kutter recommends the use of a small glass pipette, shaped like a funnel, and turned up at the bottom so that a little water may be injected at will through its narrow extremity, placed in a small hole in the roof or edges of the apparatus. These 'Lubbock nests' are in very common use.

Wasmann has combined and complicated Lubbock's nest as follows: He first unites it through a glass tube with a second or *accessory nest*, horizontal like itself, but smaller and in the same plane. The first or central nest is then connected by a second tube with two Florence flasks placed vertically one upon the other; the *upper* nest, opening at the bottom into the lower or *ante-nest*. Two tubes, curved downwards, pass through a cork and connect the upper nest with the manger on one side and the 'dumping-ground' on the other. Wasmann filled the ante-nest with earth, for the use of the ants; he even added a wooden rod, to help them to climb to the upper nest, which was also provided with a rod. The aim of these complications is to give the ants much more liberty in their movements, as well as more adaptability for different purposes. The ants are able to profit by them, as we have seen in Chapter II, Part II, in Wasmann's admirable experiment with *F. sanguinea*.

Charles Janet invented another sort of apparatus, representing a complete artificial nest, carved by the experimenter himself out of plaster which had hardened after being wetted as sculptors moisten their plaster for casts. The advantages of the hard plaster are that it supplies a regular gradation of continuous moisture, and also dispenses entirely with earth. I have made one of these in a primitive wooden mould. It is 59 centimetres long, 14 broad and 5 high, and I have carved five compartments in it, about 8 millimetres deep. The whole is covered by a glass plate, which is movable and perforated with two round holes, but set in cement in order to make sure the ants do not escape. All the compartments are inter-connected by short galleries. One serves as a manger, another as a receptacle for refuse. At one end of the apparatus is a depression, 3½ centimetres deep, forming a basin into which water can be poured. This basin occupies 7 millimetres of the total length, and does not communicate with the ants' compartments; the water filters through the plaster, but less and less as you go farther away from the basin. The compartments of the nest are covered with cardboard when desired. I have made but little use of this apparatus, as I constructed it too late.

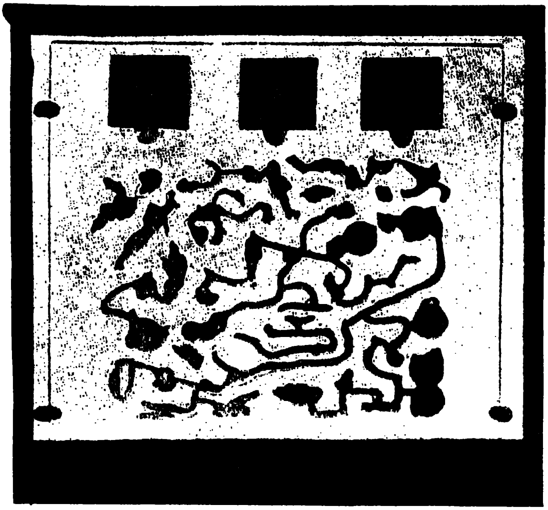


Fig. 68

Fig. 68 represents a vertical Janet nest, which can be hung up at an exhibition or in a zoological garden, so that all the visitors can observe the home-life of ants. The three square openings at the top represent a dining-room, a water reservoir and a dumping ground for the ants. All three communicate by a small internal passage with the chambers and galleries of the nest, which can be seen underneath, artistically constructed not by the ants but by the maker of the apparatus. In order to render these Janet nests more solid and more portable, Janet embedded them in zinc.

In 1900, Miss Adele Fielde constructed a nest entirely of glass, represented in fig. 69. The nest is horizontal and the glass panes are firmly cemented, except for those which roof over the two chambers composing the nest. A sponge *S* preserves a humid atmosphere in the principal nest, whose other compartment contains 'food' and constitutes the manger. A second and smaller nest, with two sponges, is depicted on the right. Some others have three compartments. Miss Fielde moved her ants from one nest to another and always washed her apparatus once a week with warm water and soap. She did the same with the sponges, having previously immersed them in alcohol. In this way she provided methodically against the growth of mould, and was able to preserve her ants alive for several years in the apparatus. We shall return later on to her excellent observations.

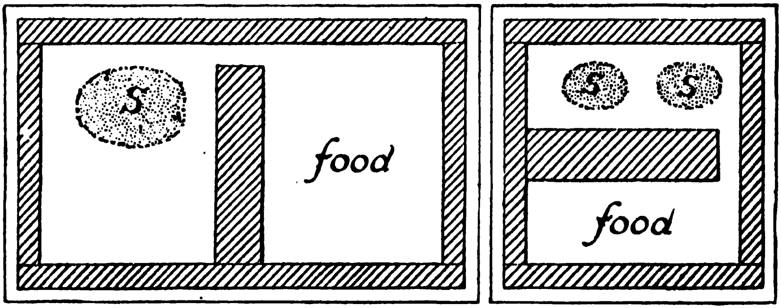


Fig. 69

Wheeler tells us that he has used with considerable success a combination of the Janet and Fielde nests, as indicated in fig. 70. The glass base is replaced by a single thin block of plaster of Paris, cast in a single piece, coloured and varnished, 25 centimetres long and 20 broad, but the height and arrangement of the chambers, their communications, the towelling and the roof panes, are those of the Fielde nest. *r* shows the plaster of Paris base, *c* the entrance, plugged with cotton after the admission of the ants from a Forel arena. At *m* we see a glass roof-pane, resting on strips of Turkish towelling (*s*), while *a* represents the opening between the two chambers, *n* a small depression serving as a manger, and *e* a slice of sponge, which is kept wet. Fig. 70 is copied from Wheeler.

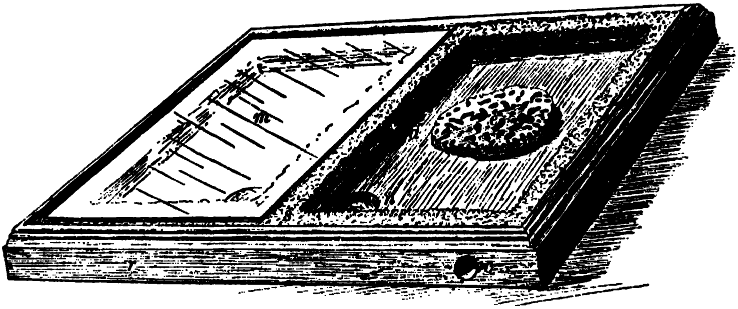


Fig. 70

To observe very small ants, Santschi constructed a minute glass nest framed in plaster. On the middle of a glass plate he modelled two small roofless chambers with plaster which had not yet hardened. Then he placed on top a second plate with its surface oiled, and pressed upon it until there was only a space of 1 or 2 millimetres between the two glass plates. As soon as the plaster is set, the upper plate can be divided in two, so that each of the chambers may be covered separately. This apparatus is so shallow that it can be placed on the stage of a microscope, like a slide. In this way, all the movements and actions of the ants can be observed directly under the microscope.

I will now borrow a description of Brun's apparatus from Kutter of Zürich, *Gehe hin zur Ameise* (Go to the Ant, Berne, 1920).

Brun makes use of the slabs of peat to which insects are pinned in a collection-case; they are 25 centimetres long by 12 broad and 1-1·5 thick. Brun surrounds the border of one of these slabs with strips of flannel, so that the peat is hermetically sealed. On the upper surface of the slab he then scoops out some chambers suitable for the use of ants, leaving them a little floor of peat at the bottom. But the whole thing is afterwards covered over with glass, top and bottom, as in the Fielde nests, etc., the upper glass panes being movable. A funnel-shaped pipette (see Lubbock nests) is sunk into the peat on one side at its thin end, and serves to supply constant moisture to the apparatus, which is thus very simply completed. The Brun nest is very cheap. The ants may scoop out the peat for themselves, according to their fancy; but at times, if too much light is allowed to pass through, they may darken the glass, always by means of the peat. These nests are not very durable and can hardly be used for several formicaries in succession, but they have this advantage, that they can be very quickly made, as the peat slabs required are commercial articles. Kutter has combined the Brun nest with the Lubbock nest, putting peat instead of earth in one of the latter kind, and making chambers in it.

Meldahl has brought the construction of the Janet nest to an extreme of perfection; but we should wander far afield were we to enter into such details here, and I will refer the reader to the exact description given by Kutter in the work cited above. Meldahl runs the plaster directly on to the glass, to a height of 3 centimetres, into a shape very carefully constructed from a cardboard model, but in a hard wood where details are wanted, which must be separated from one another. He adapts the height of the chambers to the size of the ants, allowing about $\frac{7}{10}$ of the ant in question as the height of its apartment. Everything has then to be regulated to suit the largest ants, including fertilized ♀, for which, however, the height can be reduced to $\frac{5}{10}$ or $\frac{6}{10}$ of their length. All the chambers are separately moulded in advance, and before the plaster is poured in every mould is smeared with vaseline. When all is set, the observer himself pierces the exit-holes in the plaster. In this way insterstices between the glass and the plaster are avoided, and it is made impossible for even the smallest ants to escape.

Meldahl recommends that the plaster should be saturated with salicylic acid, and a separate dry nest constructed as a manger; all this is designed to prevent mould, which is the greatest inconvenience of the Janet nests, whereas according to Kutter, it very rarely appears in the Brun nests.

Lastly, Kutter has combined the Janet-Meldahl nest with the Brun nest, by placing peat inside a Meldahl nest, which serves as an outer box; a large external compartment of plaster contains the peat in which Kutter shapes the details of the nest.

All manner of combinations can be made from the various kinds of apparatus described or at least briefly indicated above. The reader will readily discover them, and I beg him, in particular, to give a little further consideration to what I have just said about the combinations which Wasmann has added to the Lubbock nest. Needless to say, these combinations, and others also, can be obtained by adding tubes to the Janet, Fielde, Brun and Meldahl nests, etc.

Just recently, Kutter and Meldahl made a new and very ingenious combination. Replacing my arena of powdered plaster by a very large box with low sides, such as pictures are packed in, they arranged in a free but a loose, sloping piece of glass smeared with oil above and beneath, inside each of the four sides, so as to prevent the ants from passing over. Each piece rested on an interior frame, oblique like itself, adjusted to the upper edge of the box; but the oiled glass sheet was 2 cm. broader than the frame. The bottom of the box, which had no lid and was 80 cm. broad and long, formed the arena, covered with earth, sand, etc., thus imitating a natural floor. Outside the box and the glass sheets, Kutter placed at each of the two extremities of the artificial arena thus constructed, a small Meldahl apparatus which led a small tube into the interior of the arena and the glass sheets, through the wood of the box. By this means, Kutter brought about a state of war between two little enemy colonies, apparently by accident, but, in fact, deliberately, with a special end in view. He put thousands of large ants into an arena of this sort; but not one of them could cross the oiled sheet of glass.

This experiment of Kutter's, which we shall discuss later, opens new horizons to us. Imagine an arena closed in this way, but still larger—several yards square—the bottom being covered with a layer of earth which is watered and planted with grass. You will then be able to make a number of experiments on a still larger scale, in the habits of ants, warlike as well as peaceful, causing our little friends to go unsuspectingly where you please. Here I merely wish to give you some idea of the arena devised by Kutter in order to study the hitherto unknown instincts of *Strongylognathus* *alpinus*. As you know, one idea brings others in its train, and from the shock of ideas the light flashes forth.

2 **Expeditions.** In connection with my first apparatus, I have already spoken of the two instruments most indispensable to every observation, excursion or journey of a myrmecological nature—that is, having ants for its object. We must begin by saying that ordinary excursionists, Alpine-climbers and others, are not very fond of us. They want to amuse themselves and admire the view; we want to search and observe. When we stop near a formicary we annoy them, and their indifference to the observations which enthral us is scarcely less annoying to us. Thus I advise you, dear reader, if you develop such a passion for ants that you devote a journey or an excursion to them, to go alone or else secure some companion who has also a great love for them. Do not hesitate to take your midday meal with you, so that you can always pic-nic on the grass, as I generally do. Burden your back with a good wallet and your sides with a flask of water or tea (no alcohol of course!), especially in the deserts and savannahs.

But that is not enough. Alcohol, which kills men by slow degrees, is an excellent means of killing ants immediately. Fill from twelve to a hundred *strong* glass tubes, therefore, 10 to 12 centimetres long by 12-20 mm. wide, with alcohol of at least 70% (the stronger the better), according to the duration of your journey. You will thus be able to gather ☿,♀,♂ and ♃ specimens of various doubtful and perhaps new species, and separate them from one another. To save space, moreover, you can even separate the ants in the same tube by putting a little wadding between them. You will always need to have a small box with you, containing a little wadding, and do not forget a pencil and a note-book, so that you can make labels to put in the tubes, and also jot down your notes and observations.

You must also take the following objects with you: a few good ant-bags (see above), a white cloth to spread on the ground, wherein the ants you take in a hurry can be provisionally poured, so as to prevent the winged sexes, in particular, from escaping; one or two fine watchmaker's pincers, one or two good lenses, magnifying ten to thirty times, with which to examine the ants you find, especially the small ones. All these objects are indispensable. But above all, never forget your glass or your pincers when you have laid them on the grass or in a thicket, or you run a great risk of never finding them again! When you want to take a whole colony for an experiment, or to put into an apparatus, you must approach it suddenly and be decisive as well as quick in digging your chisel into the ground ; otherwise you are likely to lose a good proportion of the brood and the winged sexes, which the ☿ bury no less quickly in the subterranean passages.

You will do well, furthermore, to provide yourself with various boxes and even with a flask with a large cork pierced by a small tube, wherein to put live ants, afterwards stopping up the tube with wadding. An umbrella can also be very useful when turned upside down so that the branches of trees can be shaken into it. By this means, for example, I discovered the new *Temnothorax Antigoni* at Coccarinali, near Smyrna. Finally, you may as well also take with you on your journey a small apparatus, strong but portable, if you have time to get a colony of ants into it and feed them, and have room in your travelling-bag.

If you are only taking a short walk or a journey of one or two days, and have a garden at home in which you can establish a colony, you may secure one in a bag and bring it to your garden, especially if the species in question is interesting in its habits and is not found anywhere near your house. But in that case there must be no aggressive species such as *Tetramorium cæspitum*, *Serviformica cinerea* or *Lasius niger* swarming in your garden, or woe betide the new-comers! Now let me mention a few possibilities for excursions and journeys. A cycle can be of great assistance in shortening the long roads of a plain and bringing you to the foot of the mountains; I have even brought back on mine a whole colony of *Strongylognathus Huberi*, taken at Fully in Valais, and I established it at one time in my own grounds at Chigny near Morges, 80 kilometres from its old nest.

Nothing is more delightful than going on a myrmecological excursion in the Alps by oneself. Down in the lower Alps, the forests are full of *Formica rufa*, *truncicola*, *exsecta*, etc., according to the locality, with their guests and satellite ant, *Formicoxenus*. You will also find the large *Camponotus* coming out through holes from the nests which they have sculptured in wood. In the orchards, again, you will find *Formica pratensis* and *sanguinea*, while *Polyergus rufescens* remains down below in the plains near Geneva and Morges or St. Maurice. Leave *Lasius*, *Myrmica* and *Tetramorium* alone, to swarm on every side. Beside the streams you will see the polycalic formicaries of *Serviformica cinerea* and *Neomyrmà rubida*; and then, under bark and in dry stems, you will discover *Leptothorax*.

You are now at a height of more than 1600-1800 metres. Here everything soon changes, and your Eldorado lies under flat stones of medium size; *Formica*, *Myrmica*, *Leptothorax*, *Tetramorium*—they are all there under the stones, except a few *F. rufa*, *exsecta* and *pressilabris* under domes, which soon disappear when you get higher up. There you will discover *Strongylognathus alpinus* at Zermatt, *Myrmica sulcinodis* and *Harpagoxenus sublevis* in the Engadine, *Myrmica myrmicoxena*, maybe, at Anzeindaz, and *Leptothorax tuberum* and *acervorum* everywhere, amid a gorgeous Alpine flora. Raising your head from time to time, you will be in ecstasies over the beauty of the Alpine landscape around you just as much as the ordinary tourist who laughs at you; but you will have no need to hire a guide, as he does, for the pleasure of going and breaking your neck on dangerous ledges. A good map suffices, as a rule, to keep you clear of troublesome rocks and perilous moraines.

Now let us go through an Alpine pass and reach the South, Ticino and the valley of Aosta, as I did in 1914 with my young fellow-collector, Kutter. Here the fauna changes. *Pheidole pallidula* appears in the stony regions and *Cremastogaster scutellaris* in the chestnut trees. *Ponera coarctata* becomes frequent, and *Messor structor* gathers her seeds. Beneath the chestnuts you will find *Formica gagates* with her shiny-black body and regular gait. If you are lucky you will find *Temnothorax recedens* or *Myrmecina Kutteri* in a wall. In any case, *Lasius myops* and *alienus* will be frequent, as well as the great *Camponotus vagus*, not to mention *C. lateralis* and *æthiops*, which you will already have found, in addition to little *Plagiolepis pygmæa*, in the northern part of the Alps—the localities described as xerothermic—or *Tapinoma erraticum* of the plain of Vaud, etc. Lastly, the little greyish *Bothriomyrmex meridionalis* will certainly be found under some stone, with or without the ant which was the mother of her first colonies, that same *Tapinoma erraticum*.

Let us now cross the frontier of Switzerland. I will not trouble you with the northern countries and their monotonous fauna. In Norway and Sweden, for instance, I have found no species which is not abundant in the Swiss Alps;

though there they are found in the plains or the valleys. So let us betake ourselves merrily to the country of Tartarin de Tarascon, the fair South of France. Here the cycle will again come to your assistance, as it did to mine, in crossing the great burning roads. You will discover new species here, while the *Formica* of our Swiss forests and our northern *Lasius* become rare and disappear. In their place we find *Messor barbarus*, together with *M. structor*. You will see her gathering her seeds from bushes and afterwards burying them in the earth within her granaries. *Camponotus cruentatus*, *sylvaticus* and *massiliensis* will be found in the earth, along with *C. æthiops*. If you are lucky and very observant, perhaps you will here catch sight of *Camponotus universitatis*, a parasite of the *æthiops*, which I discovered at the time of the jubilee of the University of Montpelier. Then you will find the little *Proformica nasuta* under some rock, as well as *Leptothorax angustulus* and *niger*. *L. luteus*, on the contrary, will be on the trees. If you search carefully you will probably discover an *Oxyopomyrmex* nest. Side by side with *Cremastogaster scutellaris* and its nests, which are sometimes made of carton, little *C. sordidula* lives in the earth. You will be surprised when you see the first of the diverse southern variations of *Tetramorium cæspitum;* and besides the giant race, *T. forte*, you will notice very small varieties, *semileve*, etc.

If you go next to Italy, as soon as you reach Venice you will find *Monomorium minutum* in the grass, the carton nest of *Liometopum microcephalum* in the oak-trunks (fig. 60, Part II), *Aphænogaster testaceo-pilosa* in the woods or under the stones, the rare blind *Stigmatomma* in the Etruscan tombs and little *Cardiocondyla* on the sand of the seashore near Naples, not to mention various rare species discovered there by my friend and colleague, Professor Emery.

On the eastern side, if you move on as far as Corfu, Greece, Salonica, Constantinople and Smyrna, you will learn to recognize still other ants, especially *Cataglyphis orientalis*, with her craters and her long legs, the large black *Camponotus* species of Greece, *Messor Œrtzeni* of Salonica and Smyrna, *Prenolepis nitens*, *Holcomyrmex dentiger*, which I myself found in a meadow at Corfu, etc. The slender *Acantholepis* abounds in the rock-fissures, the sand and other places, sometimes in meadows, and divers varieties of *Cremastogaster Auberti* and *sordidula* in the earth. At the Bosphorus you will find the beautiful *Paussus turcicus* as a guest of *Pheidole*. But here, in particular, you must beware of superstitious people, who will take you for a wizard. Tell them brazen lies about looking for ants as medicine—that is the only way to quiet their stupid suspicions. Science, to them, is mere jugglery.

On we go now to Algeria and Tunis, whither I have already made three journeys, each a good month long. Here it is in the Arab cemeteries, which the novice can scarcely distinguish, and also in the mosques, that the greatest caution is necessary; while in the former you must be careful never to raise a stone. In this country, farewell to the *Formica*, *Lasius* and *Myrmica*, except for *Lasius myops* and a few rare colonies of *F. fusca*, *L. niger and M. rubra*, imported from Europe. Several faunas must be distinguished here—that of the cultivated land, that of the steppes, that of the oasis and that of the deserts, whose dunes I have visited near Biskra.

The cultivated areas are full of *Messor*, *Aphænogaster*, *Pheidole*, *Cataglyphis*, *Acantholepis*, special *Bothriomyrmex*, *Cardiocondyla*, *Monomorium*, little *Solenopsis* living in lestobiosis, etc. There are numerous species of *Cremastogaster* and *Leptothorax*, especially the latter. Some, such as the races and varieties of *Cr. Auberti*, *L. Bugnioni*, *Rottenbergi*, *nigrita* and *oraniensis*, live in the earth or under stones. others on trees or in bark—*Cr. scutellaris* in the cork-oaks, for instance, and *L. Trabutii* and *convexus* in the forests.

The home of *Messor barbarus* is, strictly speaking, in cultivated areas, and directly the soil becomes dry she is replaced by *ægyptiacus* and kindred races, whose large ☿ are much smaller in figure and head. I will remind my readers of *Thorictus Foreli*, which sucks the scapes of the antennæ of *Cataglyphis* in Algeria. In the fields thereabouts, certain *Aphænogaster* play almost the same rôle as our European *Formica* and *Lasius*.

In 1893 I brought from Algeria to Zürich a living colony of *Cataglyphis altisquamis*. When they were pursued in the garden of the sanctuary at Burghölzli by our little *Lasius* and *Tetramorium*, which entered their nest through its large opening, designed in the Algerian fashion, these large African ants *gradually learned to change their mode of procedure*. The raids of the *Lasius* first induced them to make their exit-hole narrower. But it was not until several months later that they finally *blocked it up* entirely throughout the day, as several European ant-species do. They then made shift with a small temporary opening when they went out on a sunny day—a notable contrast to their large Algerian holes and craters, open to the sky. Yet there are writers who still deny that ants have the faculty of learning by the experience they acquire! In Algeria I have brought about violent battles between various colonies of *Cataglyphis megalocola;* every enemy tries to decapitate her adversary.

While on the same journey to the province of Oran I discovered *Myrmoturba erigens*, whose curious movements instinctively imitate, to a remarkable degree, those of *Cataglyphis*, particularly *C. mauritanicus*. This may be seen when the ☿ is annoyed and raises herself on her long legs, stiffening them as she lifts her abdomen and thrusts it up in the air. She then adopts a menacing pose instead of fleeing into hiding, as other species of *Myrmoturba* will do, or at any rate, she flees into hiding less promptly, and with a more dignified air.

While *Myrmoturba Atii* lives at an altitude of 1,000—1,700 metres, in the oak-forests on the Atlas Mountains, *M. Atlantis*, which is of a light yellow colour, dwells in more open places under stones or in the cracks of rocks, at a height of 1,000—1,700 metres. In the old Roman observatory at Tebessa, on the top of Djebel Ozmor, I discovered *Leptothorax Delaparti*, which forms a transition to the subgenus *Temnothorax*.

Nearly all the *Cataglyphis* make wide open craters, even small species like *albicans* and its varieties, which are timorous and flee as soon as they are approached, even when they go in and out of the craters in large numbers. But they are quite different from *C. Diehli*, one of whose nests I discovered at Biskra, after some effort, by following a ☿ laden with a termite, her prey. I followed her for a long time in her swift, straight course. All of a sudden she disappeared into a round hole, about 1½ centimetres in diameter. Holes of this sort are very numerous in the steppes and provide multitudes of insects with dwelling-places. There was no trace of a crater or a dome. I had always to wait a few minutes before I could see other *C. Diehlii* go in or out of the same hole. They never stopped, but flitted in and out with uncommon precipitation, each one independently. At last I decided to dig my chisel into the ground. The labyrinth of the nest, containing the brood, proved to be about 40 centimetres underground. I discovered a second nest under the same conditions.

C. Diehlii has already ceased to live in the cultivated parts of Algeria; she belongs to the fauna of the rocky steppes, like *Messor barbarus* of the *ægyptiacus* group, *Aphænogaster rupestris*, various *Acantholepis*, and the small sand-species of *Leptothorax*, which we have mentioned (*Lauræ*, etc.) Here also resides *Dorylus* or the visiting ant, which makes its insect-raids at night or under the sand. While digging I have often found a number of corpses, bearing witness to their frays with other ants, *Cremastogaster* and others, but their provisional nests eluded me. To this fauna also belongs *Paraformica Emmæ*, which I discovered in the steppes around Biskra, while my wife, to whom I dedicated it, was sketching camels at pasture. This very interesting species forms a transition between *Formica* and *Cataglyphis*. It nests in the sand; its slow walk and the fact that it does not raise its abdomen connect it with *Formica;* but its external anatomical structure places it very near *Cataglyphis*. Close by I also took *Monomorium gracillimum*, *Cataglyphis albicans*, *Myrmosericus micans*, etc., etc.

Next comes the fauna of the oasis. Here there are plenty of large *Cataglyphis* and *Dorylus*, which I was shown in their sand-homes by an Arab, in recompense for a medical consultation which I gave to a young negress, his slave, in the oasis of Gabès. The oases of Algeria and Tunis also shelter in their sand a very large species: *Myrmoturba thoracica* (var. *oasium*), a smaller variety of which (v. *minor*) is found at Biskra. Apart from these, I found nothing special in the oases; their fauna was partly that of the cultivated districts, but poorer, and partly that of the steppes.

Finally we reached the desert itself, of which I have seen scarcely anything myself, except its borderlands in the dunes of Biskra, and between Gabès and El-Hamma. The curious *Messor caviceps*, *Holcomyrmex Lameerei* and *Chobanti*, which all have heads concave at the back and furnished with psammophores to gather grains of sand, are eminently adapted to the desert. But of these I have, myself, found only *Proformica Kraussi* of the Sahara, which, as it happens, has no psammophores. On the Biskra dunes, on the other hand, I have observed: *Cataglyphis* (*Machæromyrma*) *bombycina* which will be depicted in our coloured Plate I, Part V, *h* (☿) and *i* (♃). The ☿ could be seen filing along like silvery arrows on the sand of the dunes, so that a swift flash was all that could be distinguished. I succeeded in discovering a nest with a sand dome, but no crater, in a plant-tuft. While scooping it out I received some painful bites from the enormous mandibles of the ♃ hidden within. They never come out, and are not covered with the beautiful silvery pubescence possessed by the ♃. We shall speak of their probable rôle in Part V. The dome of this carnivorous hunter has several openings, like that of our *Formica.*

A few more words are required as to my travels in America, of which, however, I have already spoken, in connection with various species and facts. In the summer of 1899 I went to Canada and the Eastern United States. Directly one arrives, one notices that the green hue of the vegetation is at the same time much more bluish and much more varied than our own. One searches in vain for the earth-domes of our ants, save, as I have already mentioned, at Niagara. But the richness of the fauna makes ample compensation for these details. As you saw, dear reader, in Chapters I, VI and VII of Part I, in connection with phylogeny, geography and fossils, the fauna of North America is much richer than our own, from which it has been separated only since the Glacial Period. It includes, apart from a host of special species, simple *races* or *imitations* of our European species, but in much larger numbers. For example, we have only one *Raptiformica sanguinea;* in the United States and Canada you will find five different races, and what is more, three kindred species which are also slave-makers; and so forth.

There, in spite of Wheeler's numerous fine discoveries, I was able to find some new species, such as *Acanthomyops Murphii* and *Solenopsis Pergandei*, both in North Carolina. True, Wheeler took his revenge by finding *Strongylognathus alpinus* at Zermatt in Switzerland. *Pogonomyrmex* will display to you some very interesting granivorous habits, and you will also find the American *Messor* or *Novomessor.* Southwards, the fauna becomes richer and richer, and merges by a gradual transition, without any sharp division, without the intervention of sea or desert, in the tropical fauna of Central America. While climbing Mount Mitchell, the highest peak in the Alleghanies, at a height of 6,500 feet I was able to admire the rhododendron trees and the beautiful virgin forests of these sparsely populated countries, below which the *Attini* with their fungus gardens were already beginning to appear. But I must stop; to-day, everyone goes to the United States.

It is very different with tropical America, where I visited the Antilles and Colombia in January, 1896. Have courage, friend reader, and fear not, if you have the opportunity, to brave the untrodden forest and its wonders, in spite of its mosquitoes, mites, malaria and alligators. By avoiding alcoholic drink and arming yourself with a good mosquito-net and a hammock, both portable, not forgetting a butterfly-net and your ant-instruments, you may camp, after a ride on the back of a mule or an ox, in the air of the forest and even climb its mountains, provided you have a good guide and take your victuals on a special mule. You must not bathe either in the lagoons or in other crocodile streams, and at night the jaguars will flee from your snore as I trow they did from mine.

The recollection of my three months' visit to Colombia, on the slope and flanks of the magnificent Sierra Nevada of Santa Marta, with its giant trees, its *ceibas* and its virgin forest, will ever remain the fairest memory of my life.

On this journey my colleague Santschi, who accompanied me, acquired a taste for ants by watching me at work, and became a myrmecologist. But if you are afraid of such an adventure, you will find similar ants, without incurring any danger, at Panama, Trinidad in the Antilles, and even—though the fauna there is much poorer—in the islands of Porto Rico, Jamaica, Guadeloupe, Martinique, St. Vincent and Santa Lucia.

I have already told you how I discovered ant-nests in dry stems up on the savannahs, and I have shown you various *Azteca* nests. But you can have no idea of all the ants which are crowding down there in the forest. At every step, almost, you find new ones, if not always new species; here in the earth, there under the leaves, there under the bark, there in the air on a branch, and there again in a Cecropia-trunk.

Above you, perched on the high, soaring trunk of a Cecropia, you see a beautiful carton nest, and you wonder how to get at it. You ask your Creole guide to cut down the tree with his machete; in the virgin forest, the land has no owner, but Pan is there. Amid spines, 10 to 20 centimetres long, you struggle towards the fallen Cecropia, and find the nest of a new species, *Azteca Lallemandi*.

The *Azteca* ants are minature monkeys in the tropical virgin forest of America. They apparently consider themselves the mistresses and rulers of the forest trees, some of their nests being in the trees and some on them. I assume that the nests of *Azteca velox* and *instabilis* are made of carton in the hollow interior of large trees, where these species run about the bark in myriads, as *Dendrolasius* and *Liometopum* do in Europe. But the question is, how to take possession of them without felling these giant trees. Would that I could have been present at such a felling! What treasures I should have found!

Here you see a nest of *Atta cephalotes* or *lævigata*, guarded by the enormous head of a large ♃—a true soldier—while an army of medium-sized workers is returning home laden with freshly-cut green leaves. Some distance away is an army of *Eciton hamatum* with its ♃, armed with long hooks (see Part I, fig. 3 *B*), bound on a destructive expedition, and the insects are fleeing before it; but at the foot of their tree some *Azteca instabilis* valiantly attack them, sprinkling them with the secretion of their anal glands. On the ground in another spot you see some brown *Ectatomma ruidum* coming out of a little hole on a level with the ground, each to her solitary chase, while the big *Ectatomma tuberculatum* is doing the same on the bushes. From your seat on the mule you will catch these last-mentioned ants with your butterfly-net, as well as many other interesting species.

But now your mule stops in front of a tall tree which lies athwart the ancient track of the Indians, though little do you dream as you traverse it that it dates from before Christopher Columbus. As your guide can neither jump over the brushwood and spines of this tree nor pass under them, he must needs cut them off in order to get round it, while you are admiring another upright parasitic tree, twining around a tall, unfortunate palm. In other places, the enormous aerial roots of *Phyllodendron* hang from trees 20 to 30 metres high. On the ground, while you are waiting, you discover a new species of *Sericomyrmex*—*S. Diego*, with its fungus gardens.

In the clearings, *Pheidole*, *Cremastogaster*, *Stecomyrmex* of the old trunks, *Neoponera stipitum* of the dry stems, etc., etc., will delight you and console you for the itching caused by the mosquitoes and garapates. And at six o'clock in the evening, after making a frugal supper at your camp-fire on the rice and roasted 'platanos' (common wild bananas) you have brought with you, and after catching on the wing some luminous click-beetles, lured from their nocturnal amours by the piece of burning firewood you shake before them, you will sleep peacefully in your hammock, stretched between two forest trees, well protected by your mosquito net, which stretches in its turn over you. When you wake next morning to continue your travels in the Eldorado of ants, you will experience a feeling of ineffable freedom, of aloofness from war and the paltry hatreds and jealousies of men in their towns and villages. More and more will you appreciate the social anarchist-communist system of the ants; and then you will regret that we, alas! are forever incapable of imitating such a social system.

Chapter II

NUPTIALS. FOUNDATION OF COLONIES

a NUPTIALS

When the ♀ and ♂ have emerged from their pupal skins and cocoons, inside the nest, they lead at first an idle and useless life. They allow the ☿ to disgorge copious supplies of honey-dew to them, or at the very least, as in the case of the *Ponerinæ*, to give them tit-bits in the form of insects. In our climate, if they are hatched late in the autumn they sleep through the winter. But in warm countries, and in our own when they are hatched in the fair-weather season, their strength increases, their wings—when they have them—grow more substantial, and amorous passions stir within them.

As a rule, these passions have no great power as between brothers and sisters of the same formicary; which, more often than not, remain chaste until the time of swarming. But there are exceptions worthy of our study.

Here, dear reader, you must permit me to digress. Science is in the habit of devising and combining at will, for frequent use and abuse, big words with Greek *roots*, that is, with Greek terms as their foundation. For instance, certain Greek roots have the following meanings: *adelpho*=brother, and sister; *gam*=marriage; *phag*=to devour, eat freely; *Myrmex*=ant; *genes*=origin, genesis; *onto*=existing; *phylo*=lineage, race, conservation; *phil*=friend; *phyllo*=leaf; *poly*=

numerous, several; *morph*=form; *log*=word and science; *pleo*=rich in; *metr*=matrix and also measure; *anthropo*= man, etc., etc.

You will now understand the meaning of the following words, which we have already used or shall use later on: *Myrmecology*=science of ants; *adelphogamy*=marriage between brothers and sisters; *adelphophagy*=eating one's brothers and sisters; *anthropophagous*=man-eating; *polymorphism*=numerous forms; *pleometrosis*=rich in matrices, that is, in females; *myrmecophiles*=friends of ants; *phylogenesis*=genesis, preserving the race or line; *ontogenesis*= genesis of individual existence, etc.,etc.—big Greek words are really no more fearsome than that. With a good Greek dictionary, you can make some more for yourself, without even knowing Greek or its grammar; a knowledge of the Greek alphabet is enough. After this, *revenons à nos moutons*, that is, to our ant-nuptials.

The first special case is that of certain rare and very scattered colonies in which there are only winged ♀ and ♂ deprived of wings from the time of their hatching. This is the case with *Anergates atratulus*, a European parasitic ant, whose worker has disappeared. Here marriages take place, in the nest itself or at its surface, between newly-matured brothers and sisters sprung from the same mother, for there is never more than one queen-mother. Hence this is a clear and evident case of perpetual and constant *adelphogamy*; at any rate, no exception has hitherto been discovered. It is possible, moreover, to observe these weddings or copulations at one's ease, if one arrives at the right moment. The numerous ♀ do not raise any objections; they are even very encouraging to their numerous husbands, who display as little jealousy towards one another as those of the aerial nuptials, which we shall discuss next. The husbands go about the business of mating in a very heavy and very clumsy fashion. The ladies fly away directly their seminal vesicles are sufficiently full of sperm, and certainly make straight for their host, *Tetramorium cæspitum*, which they induce to adopt them, but so far no one has been able to see just how they manage this. However, certain fertilized ♀ of *Anergates*, which Crawley and Donisthorpe introduced in 1915 into a strange colony of *T. cæspitum*, each seized and held fast to one of their ☿ hosts by an antenna, and so saved themselves from being attacked meanwhile. One of them was then adopted by a colony of *Tetramorium* which killed all their own ♂ and ♀. After their marriage, the *Anergates*' husbands do as the other ♂ ants do—they perish.

But, however true it may be that all the products of adelphogamy have but a single mother, we cannot ignore the fact that they have divers fathers. These fathers are all brothers—of that there can be no doubt—but their individual differences may be of value to their children; which is not the case with the brother and sister marriages among us mammals, whose women-folk do not possess different seminal vesicles for different husbands. Furthermore, the constancy of adelphogamous marriages in the phylogeny of *Anergates* is a phenomenon the like of which is as yet unknown in nature.

Nearly all species of the genus *Cardiocondyla* have only winged ♀ and wingless ♂. But here the conditions are different from those obtaining with *Anergates*. In the first place, the colonies are not far away from one another. Again, they are not parasitic upon other ants, and possess ☿. Finally, pleometrosis, which means the presence of several ♀ in one formicary, is found occasionally in this genus. But so far as I am aware, no one has observed the mating-process of *Cardiocondyla*. On the shores of the Black Sea, I myself have taken the pale yellow ♂ of *C. Stambuloffi* inside the nest with their dark-coloured ♀ and ☿. Santschi has done the same in Tunis with *C. Batesi* v. *nigra*, which presents almost the same differences in colour between the ♂ and ☿ as the species previously mentioned. In view of his pale colour, therefore, it would seem that the ♂ does not leave the nest and must be adelphogamous like *Anergates*. But in that case we must suppose that the ♀ utilizes her wings solely in order to fly off and found a new colony on her own account, either in the sand a few metres away, or else in another district—possibly even to go and enforce adoption by another colony. Here we have a yet unanswered problem, for nature is seldom disposed to conserve in an active form organs which have become useless. Incidentally, Santschi wrote to tell me that he had once seen a ♂ *Cardiocondyla* working like a ☿ and carrying larvæ.

The European *Formicoxenus nitidulus* (Part I, Plate III, *h* ♂ and *i* ☿) represents a third case, differing from that of *Cardiocondyla* in the following respects. Stumper first proved that it infests the nests of its hosts, *Formica rufa*, from a central point outwards, and that it also founds, inside one large *F. rufa* nest, small multiple colonies or polycalic formicaries, whose numerous queens can easily pass on foot from one to the other. Stumper observed the copulation of several ♀ with the ♂ (which were always without wings from the moment of hatching) by adelphogamy. But here the matter is still further complicated by the fact that *F. nitidulus* possesses wingless ergatogynes which constitute all possible transitions between the ♀ and the ☿. Here, therefore, adelphogamy is to a very large extent relative, owing to the facilities for change of domicile which polycalic colonies offer to numerous ♀, even the ergatogynes. Can the wings of the ♀ also be in process of disappearing?

Such a case would be unique in myrmecology. Let us shun hypotheses. Our present business is merely to ask the question.

The circumstances of *Ponera punctatissima* and *ergatandria* appear to be similar to those of *Anergates*; the only forms at present known are the ♀ winged, and the ♂ which are apterous (wingless) from the moment of hatching. Their formicaries are rare and very populous; but as yet we know too little of their habits to decide the matter. On one occasion only did I see the black *P. punctissima* ♀ flying away accompanied only by ☿ and reddish-brown wingless ♂. The same thing seems to obtain with *Symmyrmica Chamberlini* of Utah, which lives as a parasite with *Neomyrma mutica*, but resembles a ☿ as well as a winged ♀ and a ♂ which is always apterous and much like a ☿.

We have a special case in *Ponera Eduardi*, whose female is winged, but which has two kinds of ♂, one winged, the other apterous—in two different varieties, it is true. And here is a good opportunity for further investigation; the mating-process has not been studied.

Next in order are the ants whose ♂, contrariwise, is always winged, and whose ♀ is always apterous. This state of affairs is characteristic of the sub-family of *Dorylinæ* or visiting ants (fig. 107, *A*, *B*, *C*, *D*, and *E*, Part V). Unfortunately no one has yet been able to observe their nuptials, which most probably take place at night. It may be that the ♂ mate with their sisters of the same formicary by adelphogamy; or—and this seems to me more probable—that they fly away to other formicaries of the same species, to lie in wait for the virgin ♀ which come out at night from their nests, and thus brave the enemy ☿. Whatever the truth may be, we are still reduced to conjectures. Wheeler and Santschi have observed *Dorylinæ* flying out alone from their nest. Others have seen the ☿ chasing them away from the nest and thus forcing them to fly away. In other places Savage has observed ♂ which have lost their wings following the ☿ in their predatory expeditions without being molested by them, and even coming back obstinately when driven away. Wheeler thinks that the *Dorylinæ* usually have one queen to a colony. On the other hand, he assures us that the *Eciton* ☿ of Texas readily adopt strange queens. In short, this is a matter in which thorough scientific research is still required.

In *Leptogenys* (Part I, Plate III, *d* ☿ and *e* ♀), and perhaps in *Diacamma*, the winged ♀ has disappeared. She had been replaced by an ergatogyne which resembles a simple ☿ so closely that she can scarcely be distinguished except for the fact that her abdomen is distended by large ovaries. Here, again, no one has yet been able to observe copulation with the ♂, which is always winged. *Leptogenys* and *Diacamma* make large independent colonies with many workers, but their nuptials are unknown. How the colony begins, and the nature of its founder, the future must discover.

We come now to ordinary well-known facts, the aerial nuptials of the ants represented in fig. 71, after a sketch which my friend Emery once made for me. The nuptials of ants have often been compared with those of the bees, of which Maeterlinck has given us so fine and poetic a description, especially in the following passage, which refers to the queen or ♀ while yet a virgin, and the swarm of ♂ which follow her in the air.

"Drunk with her wings, and obeying the magnificent law of the species that chooses her lover for her and wills that the strongest alone shall attain her in the solitude of the ether, she rises and ever rises; the blue air of the morning rushes for the first time into her abdominal stigmata and sings, like the blood of heaven, in the myriad tubes linked with the tracheal sacs, nourished on space, that fill half her body. She rises still. To some lonely region must she soar, unhaunted by birds that might profane the mystery. Still upward she climbs, and now the ill-matched crowd beneath her dwindles and scatters. The weak, the infirm, the aged, the unwelcome, the starveling brood of sluggish or impoverished cities, all these renounce the pursuit and disappear in the void. All that remains is a small and tireless group, hung in infinite opal. She exacts of her wings one supreme effort, and lo! the elect of the incomprehensible forces reaches her side, seizes her, conquers her; and borne aloft by their twofold impetus, the ascending spiral of their intertwined flight spins for one second in the hostile delirium of love."

In the nuptials of the ants, however, which are polyandrous, not monogamous like those of the queen bee, everything happens in a much more prosaic fashion. Let us begin with our common *Myrmica rubra*, whose red ♀ is represented in fig. 71, with the black ♂ flying a little above her. I myself have often been right on the scene of nuptials such as these.

The marriage-flight is a great event for every formicary. As the wings of the newly-hatched ♀ and ♂ grow firmer, they become more enterprising, and the unrest in the colony increases. Not only do the winged sexes prepare themselves several days in advance before they take to flight, but the ☿ are likewise disturbed, and less busy about their ordinary occupations. It is fascinating beyond all measure to watch the unrest of the ☿ setting out from the nest, caressing the antennæ of the ♀ and ♂ as they feed them, accompanying them to the grass-blades and mounting guard over them like sheep-dogs over their flocks, as Escherich aptly remarks.

Fig. 71

This state of affairs continues for several days, according to the temperature and weather. The ♂ are usually the first to fly away, and the ♀ follow; but quite often individuals of both sexes which are hatched later than the others do not take to flight until a day or even several days later; there is no general rule; rain or rough weather may hold up the entire process for a time.

On a fine afternoon in August, for example, nearly all the formicaries in a district will act together and take part in one main swarm. Then all enmity ceases. In the flight of the ♀ and ♂, the hatred of diverse communities is replaced for a day by sublime love, reciprocal and international. In great distress, the ☿ of each formicary go along with their winged folk, which climb some blade of grass and ungratefully abandon for ever their home and their nurses; for an imperious natural instinct ordains it so. Then all are intermingled in the common swarm, which sometimes darkens for a space the blue of the sky. A roof, the topmost point of a poplar, a church-tower, the summit of a hill, sometimes even a man standing upright or walking slowly, serves as the usual basis, the rallying-place of the swarm, which gambols rhythmically in the air—keeping pace, for instance, with the man as he walks. The ♂ of *M. rubra* is almost as big as the ♀, and when he reaches one of them a hand-to-hand tussle ensues, and both are brought to the ground. But a fall is of no significance for creatures of such negligible weight. Making light of the matter, they roll on the earth together and accomplish their union. At this juncture, five or six ♂ can be seen mating with the same ♀, one after the other, without any fighting among themselves over such a trifle; one waits for a few seconds until the other has finished, that is all. After mating, they often caress one another's antennæ. All then fly away to begin the same tricks over again.

But shortly afterwards, probably the next day, the pathways, especially those round a tower, are bestrewn with the corpses of ♂ and sometimes of ♀. Once fertilized, the females which survive cast off their wings by means of bodily contortions, and then crawl away somewhere to dig out a chamber wherein to enclose themselves and attempt to found a new colony in solitary state. Huber gives the following account of a *Lasius niger* which had just been fertilized:

"I had three fertile ants, one of which I took and enticed into the apparatus; I made her go in of her own accord by offering her a piece of straw, up which she climbed, and in this way I carried her to her new home, without having touched her. Scarcely had she perceived the damp earth covering the bottom of her dwelling than she stretched her wings with an effort, bringing them to the front of her head; she crossed them in every direction, twisting them upside-down, first in one direction and then in another, and underwent such curious contortions that her four wings fell off at the same time in my presence. After this she rested, brushed her armour with her legs, and walked about on the ground, where she seemed to be looking for shelter. . . . I repeated this experiment with several females of different species, and always obtained the same result."

Huber also proved that ♀ which remain virgins preserve their wings indefinitely. The genital valves of a ♂ ant are never torn off and left hanging in the cloaca of the ♀, as in the case of the bees; he always draws them away in good condition. In America, according to Wheeler, much the same happens to *Pogonomyrmex* as to our *Myrmica rubra* and its corresponding races in the United States. Ihering declares that the large ♀ *Atta* of tropical America are fertilized while actually in the nest, by their winged brothers—

that is, by adelphogamy, but I profoundly mistrust this author.

We now come to those aerial nuptials in which the ♀ is much larger than her little ♂, and capable of carrying him into the air on her back, without falling. This happens with our *Lasius*, *Tetramorium*, and *Solenopsis*, as well as their corresponding forms in North America and Asia. It is these that form the enormous swarms of winged ants which sometimes appear in summer and darken the air with their multitudes. In this case, no interlocked couples are ever seen to fall and complete their amours on the ground. It all takes place in a poetic fashion, up in the air, sometimes at a great height, but in a most brotherly spirit, entirely exempt from jealousy.

Preparations are made in the nest and at its surface for the departure of the two sexual forms, accompanied by the ☿, exactly as we have described for *Myrmica rubra*. The strong, heavy ♀ begins by filling her whole body with air, by means of her tracheal sacs. After climbing on to a blade of grass or a stone, she then stirs her wings, so powerful yet so delicate, as though to try them for the first time. At last she decides to fly after her brothers, who have gone before her to join the great common fraternal swarm up in the pure air. Though assailed by a crowd of small ♂ from countless formicaries, whose masoned domes cover the ground on every side, our ♀ never flinches, but continues her majestic flight. I have seen more than one *Lasius flavus* and *niger* ♀ carrying two ♂ on her abdomen, while a third, perched on this same abdomen, patiently waited his turn, only to be followed by others in an uninterrupted stream. The copulation of each ♂ lasts a few seconds only, a minute at the most, and the poor little creature has achieved the sole purpose of his being.

You will ask me with a smile, dear reader, whether I have chanced to watch these aerial nuptials from an aeroplane. No; but all *Lasius flavius* and *niger* do not fly so high, and I have sometimes managed to catch a few as they were mating in the air, or even as they were settling on my hand. In connection with *Lasius emarginatus*, the process is much more difficult to observe, as the marriages take place at night. After copulation, however, everything happens as in the case of *M. rubra*. At all times and places, the virgin ♀ preserve their wings and those that are fertilized tear them off; Miss Fielde has proved this by patient and exact experiments.

But ants with winged ♀ and ♂ do not always swarm. Many of them, especially *Camponotus*, *Formica*, *Polyergus*, *Tapinoma*, etc., fly away, it is true, but for the most part separately, to unite with the members of various colonies, whether on a mound or on the foliage of a tree, rather on the ground than in the air. *Leptothorax* does the same on a small scale, and does not fly far from its little nest.

In many of these ants, experimenters have observed indubitable cases of adelphogamy—Brun, for example, with *Tapinoma erraticum* while migrating, and Escherich with *F. rufa* in its nest. But, as with men, this has little effect, for consanguinity of this sort, being more or less exceptional, can do no more harm to the species, or as we say, the 'race,' than our first-cousin marriages, provided the lineage of both parties is not tainted with hereditary disease. In ants, natural selection always kills off such diseased individuals, whereas we conserve lunatics and alcoholics in our asylums with the utmost care. And furthermore, we make an even more careful selection of healthy men for the purpose of turning them into cannon fodder, before they have had a chance to unite with any women, except prostitutes, who give them hereditary syphilis. On the other hand, modern man, who is classified as 'wise' (*Homo sapiens* L.) forbids adelphogamy—and what is more, has a horror of marriages between first cousins. But we must return to other ant-nuptials.

With regard to *Cataglyphis* of the desert, steppes, etc., Santschi wrote to me as follows: "The sexual forms in *C. bicolor* run very swiftly over the ground, where they pursue and mate with each other. The ☿ take part in the ceremony, and I often see them holding back the sexual forms by their wings. Those of the ♀ are quickly lost; those of the ♂ are relatively short, and this fact prevents sustained flight and is in keeping with copulation on the ground during motion. This takes place towards the end of spring on very warm days, and is not uncommon even in the towns, where *Cataglyphis* often nests. It is easy at these times to observe the ♂ pursuing the ♀ on the walls." Obviously, therefore, certain genera of ants mate on the ground, although their ♀ and ♂ are both winged. Thus there are clearly all manner of transitions among the ants between aerial and terrestial nuptials, and the purpose of their wings varies in the ♂ as it does in the ♀.

In Santschi's opinion, the fertilization of *Bothriomyrmex* takes place outside the nest, but he has not observed it. In *Wheeleriella*, on the other hand, it may take place in the nest, where he has seen it accomplished by adelphogamy, but it can also occur outside. Santschi has also seen the nuptial flight of *Monomorium Salomonis* and *Solenopsis Lou* in Tunis. In these two species, the ants flew to a cactus-plant or on to Santschi himself, and the same ♀ mates rapidly with several ♂, one after the other. But the *Monomorium* ♀ dismissed each ♂ with a bite immediately after copulation, so that she might give a gracious welcome to his successor. Each love-affair lasted only 30-40 seconds!

In Tunis, so Santschi writes to tell me, *Messor barbarus* ♀ and ♂ come out of the nest and mate, probably in the air, the day before the rains begin, and this has enabled him to predict rain to the Arabs a day in advance.

b FOUNDATION OF COLONIES

Though all ♂ ants perish miserably soon after their wedding, after wandering about in a forlorn condition for a few hours or days, the life of the fertilized ♀, relieved of their wings but transformed into secondary hermaphrodites with their *receptacula* full of semen, is only just beginning; it is henceforth to be a hermit-life, but it varies according to species, and we must here devote some study to various peculiarities.

In the bees, it is all very simple, and happens in broad daylight; no fertilized ♀ or queen will suffer another near her, and a troop of workers always assists in the foundation of a new hive. It is very different with the ants. In the first place, a fertile ♀ can often found a colony on her own account, without the aid of the ☿. Again, in the darkness of the nest so many different things occur, according to the genera and species, that we are still far from having elucidated everything. I will here set forth what I think about the matter.

P. Huber was the first to show the normal way in which a single ♀ may found a colony, and he also discovered young incipient colonies with the mother and a few ☿; but Lubbock, McCook and Blochmann were the first to offer more complete experimental proof in connection with *Myrmica* and *Camponotus*, while Janet dealt later with *Lasius* and *Formica fusca*, and finally Piéron with *Messor*. Huber, and his successors, including myself, have very often found a fertile ♀ ant shut in by herself in a chamber, closed on all sides, either under the ground or under a stone or bark, with or without a bundle of eggs at her side. In 1899 I found in the United States an incipient colony of *Camponotus fallax* (variety), by which I mean a fertile ♀, alone with her cocoons.

On finding a fertile *Camponotus ligniperdus* ♀ at Montricher, in the canton of Vaud, where he was staying for a short time at the end of August, 1901, my friend, Prof. Emery, brought her to me at my home in Chigny, near Morges, and asked me whether I cared to essay rearing her. I give here a summary of my observations on this ant:

She was set in her chamber in a small jam-jar. There was a piece of glass instead of the cover, with a piece of cardboard on the glass. The chamber was 22 millimetres long by about 14 wide and 10 high. I put the jar on a shelf in my workroom, adding a little water from time to time, to keep the earth damp, but making up my mind to add nothing else under any pretext whatever. My room was well warmed throughout the winter. The female *C. ligniperdus* received no food at all in her closed chamber. I left her thus without even raising the glass, until February 2nd, 1902, only satisfying myself that she continued to move, and therefore to live. I noticed the presence of one bundle of eggs at least, but I cannot guarantee that these were the ones which were there when Emery brought her to me.

On February 7th, a very big larva enwound itself in a cocoon, which was only about 6 millimetres long, or of the same size as the smallest workers, such as are found with the fertile females which are beginning a colony; but this was enough, the fundamental difficulty had been overcome.

On February 13th a second larva spun itself a cocoon, slightly larger than the first. The ♀ was lively, alert and not over-thin. The larvæ grew rapidly. There were now three of them, one being very small, but no more eggs.

On February 17th, a third larva spun a cocoon. Only two larvæ remained, one of medium size, the other very small. When I raised the glass in order to observe, the ♀ picked up a cocoon or a larva and carried it to the lowest part of the chamber. I changed the glass, as it had become cloudy (owing to the saliva, etc., of the ♀). I noticed that every time I raised and cleaned the glass, the ♀ hastened to seal hermetically the crack which separated it from the earth, by applying fragments of earth moistened with her mandibles.

February 24th.—Ever since the two largest larvæ had spun cocoons, the remaining two had obviously flourished and had grown a great deal. This day a new-laid egg was added, the sixth of the progeny.

February 26th.—Another egg.

March 1st.—5 eggs, 2 larvæ, 3 cocoons.

March 4th.—6 eggs, 2 larvæ, 3 cocoons.

Here I must interrupt my observations to discuss the matter. We have before us the indisputable fact that a female ant lived from August, 1901, to March, 1902, without any food except the water which trickled through the earth, and not only remained in a warm room, alert and well, shut in a prison from which she was neither able nor anxious to escape, but laid eggs and reared five larvæ, three of which reached maturity and were transformed into chrysalises.

What did these larvæ feed on? As I wished above all to obtain a good result from the experiment, I did not try to observe how they were fed. Moreover, my apparatus of natural earth would have been useless for this purpose. I should have needed an artificial plaster chamber made on the Janet system.

The only real possibilities are as follows:

(1) The ♀ feeds her larvæ in some fashion or other with the secretions of her body.

(2) The larvæ devour the eggs subsequently laid, as they gradually appear (which would indirectly amount to the same thing as 1).

(3) They suck up the water which trickles through the earth, and which must contain certain nutritive fragments of humus.

(4) The three methods above mentioned, or two of them, are employed alternately.

I see no other possibility.

It seems to me certain that No. 3 alone cannot suffice, but equally certain that water plays a great part in the nutrition of the larvæ; in a dry chamber all would have perished. By using an artificial chamber built on the Janet system and moistening it with distilled water, we shall find it easy at some future date to eliminate from (3) all nutritive elements except pure water—and what success we shall have then remains to be seen.

(1) and (2) amount to the same thing fundamentally, for according to both, it is always the body of the mother, and that alone, which feeds the progeny until maturity. Hitherto I have seen no larvæ devouring eggs, but according to the observations of Janet, Wheeler, etc., it is probable that they do so. It is strange, however, that the eggs should have steadily increased in number between February 24th and March 4th, in the presence of two voracious larvæ. Fischer and Schiemenz have shown that the nursing juice which bees disgorge to their larvæ is prepared chiefly in the dorsal pair of yellow salivary glands, situated under the vertex, which gland is also strongly developed in the ants (Meinert's *glandula verticis.*) The same thing might obtain with the nursing ants. It seems impossible that their crops should still contain food-substance after so prolonged a fast. All the resources left, therefore, are the secretion of the

salivary glands and the eggs. Possibly these two sources of food are utilized in feeding the larvæ. Observation and dissection will at length make the matter clear.

But Wheeler and Janet have proved, as we have seen, that the muscles of the wings, which are torn off by the ♀ themselves after fecundation, are entirely reabsorbed, within a few weeks, in the blood of their own bodies, by means of what is known as 'histolysis.' This is no negligible asset in nutrition, either for mother or children.

But to return to our *C. ligniperdus* ♀. On March 12th there was no change. The six eggs had turned yellow; one larva had become adult.

March 20th.—One cocoon had disappeared. The adult larva did not make itself a cocoon; *only two of three eggs remained.* Which had eaten the eggs—the ♀ or the larva ?

March 28th.—The ♀ had eaten one of her larvæ! The day before she ate half of it, and to-day the rest; it was the large larva. The eggs had disappeared, all except one, but to-day there was a new bundle of eggs. Hence there were more than two cocoons and one larva. The ♀ was beginning to degenerate.

April 23rd.—I had been away for three weeks. During this time, my daughter took care of the ♀, which now had two cocoons, one larva and a bundle of eggs.

April 26th.—The second larva was eaten.

April 28th.—The eggs were also eaten. The cocoons were almost mature.

May 1st.—One of the cocoons was swallowed. The ♀ was further degenerating. She became uneasy, scratched up the earth on every side, neglected the cocoons and dug in several directions.

May 7th.—A ☿ was hatched, but she was somewhat lame! The ♀ had scratched up a great deal of earth and scooped out a gallery. The other cocoon was destroyed. I placed the nest on some moss, on a tray surrounded with water, and put the whole apparatus in the sun.

May 12th.—The ♀ had become very restless. She continued her gallery and finally escaped from her cage by this means; but she returned to it of her own accord. The worker was still very pale, weak and ill-hatched, and grew no stronger. While the ♀ was away I gave this ☿ some jam for the first time. She did not touch it.

After this I was obliged to absent myself and leave everything to my secretary. The worker died on May 19th, but the ♀ herself then began to eat honey. She now became more and more restless, and set about digging in the ground in all directions to force a way out. On May 28th she succeeded. This observation, though it did not lead to the desired colony-foundation, was very instructive. In the first place it proves that a fertilized ♀ was able to remain for nine months in her cell without receiving any food from outside except water, and not only to rear larvæ and nymphs, but also to draw a nymph from its cocoon, entirely unaided, and cause it to hatch. When Emery brought her to me she had already, in fact, fasted in her cell for a certain time. As we occasionally find incipient colonies similar to that represented in fig. 55 (Part II), it is as clear as daylight that the final distress of my *C. ligniperdus* ♀ was due to my habit of continually disturbing her, and also to a method of upbringing which was artificial, or in other words, far from normal. But this very distress and the ♀'s flight also prove that the cenobite and fasting instinct is intimately connected with the foundation of colonies.

Why did the ♀ begin to 'degenerate' towards the end of April, even before she had drawn the first nymph from its cocoon for the hatching of her first ☿? It is difficult to explain, but we can and must think that she had already an instinctive presentiment of a bad end, before we could see it. Another very interesting point is the indubitable proof that a fertile ♀ which had failed to rear her brood could reacquire her freedom after nine months, dig in the earth by herself, escape and begin to eat spontaneously. In 1902 these facts were new.

In the *Revues des Questions scientifiques*, Louvain, July, 1920, pp. 14-22, Simpel wrote the history of several fertile *Lasius flavus* ♀ which he succeeded in inducing to act as the definite founders of new colonies, after suffering many mishaps and fasting from July, 1917, to May, 1918.

Under normal conditions, it is not the fertile ♀ which leaves the incipient nest. The ☿ dig a passage and go out to milk aphids and so obtain food for their mother, sisters and brood. After this the new colony is able to develop unaided and to prosper, on condition that it finds food and is not destroyed by rivals.

On every occasion, the ♀ of incipient colonies founded in this way are remarkably small, smaller than all those ☿ belonging to older colonies.

In considering the above facts, dear reader, you may well admire the marvellous adaptation of instinct to an unprecedented degree of economy which utilizes every device to enable the fertile ♀ to fast in her cell; smallness of ☿, reabsorption of the wing-muscles, nutrition by water, adelphophagy of eggs, etc. This last point was not proven by my own observation, but by those of other authors. For that matter, whether the hatched larvæ ate their little sisters which were still in the egg-stage, or the mother devoured her own eggs, the final result was the same; for in the latter case, as we have seen, the ♀ would have been better able to feed her larvæ with her saliva.

Whither was our female attempting to flee at the end of May? I ought to have profited by the occasion to place her in the presence of ☿ of her own species, deprived of their ♀, for they would probably have adopted her at once. It may have been just such a haven of refuge that she was seeking when she fled. We shall examine this possibility shortly. Janet has proved, however, that the mother queen of a colony, when taken from her brood and isolated, may sometimes found a second colony.

We have been admiring the marvels of adapted instinct and their economy. In these facts, betraying the meticulous adaptation of causes to their effects, some people find proof of an Intelligence in the Universe, divine, supreme and personal. They forget that the word 'intelligence' is only an abstract term extracted from our meagre human intelligence, and that they are only moving in a vicious circle. Science proves simply that all animal and vegetable life forms and develops in phylogenesis, as well as in ontogenesis, by the accumulated inheritance of characters which living beings have acquired, second by second, day by day, year by year, millions of years by millions of years, owing to stimulation by the action of the external world, in other words, by the engrams they receive from these stimuli. It also proves that natural selection brings about a gradual detailed adaptation of the characters thus acquired to the various circumstances of this same external world. Thus it is that living organic 'nature' reacts upon the living beings which spring from her. We are at liberty, if it pleases us, to give such adaptations the name of 'intelligence,' a quality of our own whose range, in our immense vanity, we exaggerate. This intelligence simply plays a part in the manifestations presented by living beings. But all the rest is only sophistical divagation on the unknowable 'Absolute

First Cause of the Universe' which forms the object of the grandiloquent false science called metaphysics. Genuine science gives no reply to all this but the old dictum of Socrates, 'I know nothing about it.'

The observations of Blochmann and other authors have shown the truly remarkable skill of the fertilized ♀ in digging for themselves the chambers in which they afterwards hermetically seal themselves, feeding and caring for their larvæ, cleaning them, giving them fragments of earth to help them form cocoons, then removing this earth and finally opening the cocoon so that the nymph may be hatched. And yet there are no ☿ to teach them all this. They do it alone, by hereditary instinct. But this instinct normally ceases as soon as the offspring which are hatched grow strong enough to be able to leave the maternal prison and go in search of food for their mother and her brood. The fasting and cenobitism of the queen-mothers which shut themselves up are an admirable natural adaptation of instinct. But for this, the ♀ would go away and abandon her brood, which would inevitably be devoured by other insects.

We have described above an ordinary case of colony-foundation; it might also be called the primary case, for the others are evidently derived from it. Let us now pass on to the secondary cases.

We have just seen our *Camponotus* take to eating again and then depart, after nine months of fasting, and have wondered what she would do if she were to meet ☿ of her species. But before their instinctive fast, many ♀ ants which have just been fertilized and relieved of their wings are similarly circumstanced, and while wandering about before digging in the earth to shut themselves up, they meet ☿ of their own species and sometimes even from their own colony. Lepeletier de St. Fargeau, who knew nothing of the longevity of ♀ ants, thought that this was the ordinary way in which new colonies were founded, and as early as 1810, Huber had put forward the same view with regard to the annual renewal of already-existing colonies. But these opinions were little more than hypotheses.

As a result of all the recent experimental work of authors such as Emery, Brun, Janet, Viehmeyer, Wasmann, etc., we know that colonies which have lost their fertilized mother will most readily and kindly adopt a strange ♀ instead of threatening or even killing her, as those already provided with fertile ♀ usually do. Moreover, the 'quarantines' described by Wasmann which ant-guests often endure, when they change from one colony to the other, as we saw in Part I, resemble those to which the ☿ submit a fertilized ♀ that does not belong to them. Cases vary; if the ♀ has to compete with one or more rivals which suffice for the society, she runs a severe risk of her life; otherwise she is adopted. If the ☿ she meets are a long way from the nest, they may found a new colony together.

McCook records and Ihering claims that fertilized ants sometimes go to battle with each other as queen bees do; Ihering makes this statement with regard to *Azteca Mülleri*, among others. But I place no reliance upon these two authors, and for my own part I have never observed anything of the sort.

And now we come to special cases.

Wasmann uses the term 'pleometrosis' for cases in which several ♀ are found together, living in peace in one colony. It is not maintained that they have all been there since the foundation—we have just been talking of subsequent adoption. Wasmann and Brun have shown that the fertile ♀ of *F. rufa* are very readily adopted by a strange colony. But I myself have proved that two or more fertilized ♀ often collaborate to form a colony. Crawley and Donisthorpe, for example, have described an association of sixteen fertile ♀ founders. I myself once found at Simplon about fifty fertile ♀ of *F. rufa* collected under one stone—which proves nothing much, for that matter.

Brun has made the following interesting observation. Two fertilized ♀ of *Lasius niger* were adopted by ☿ of that species, and lived together for three months in absolute peace. But one of them then became sterile, and the ☿ killed her and tore her to pieces, while the other continued all by herself to lay a mass of eggs. Janet, too, saw the ☿ of certain *Tetramorium cæspitum* and *Solenopsis fugax* colonies, containing several fertile ♀ living together in peace, destroy all these ♀ but one, as soon as he enclosed them in an apparatus of his own, which forcibly restricted their expansion.

A fertile ♀, observed by von Buttel-Reepen, in his own special apparatus, was unable to dig herself a satisfactory hermit-cell, and therefore broke into that of her neighbour which had made a greater success of the task, and even moved her own eggs thither. At first, these two ♀ lived comfortably together and brought up their larvæ conjointly. But as soon as the first ☿ were hatched the two mothers began to fight, until one of them succumbed. This interesting observation may represent the general rule, as Escherich thinks, or it may be an exception. We had better wait a little longer and not embark on hypotheses. Wasmann has given the name 'monometrosis' to cases like the above, where a species of ant cannot keep more than a single ♀ permanently in the formicary. Monometrosis is thus the opposite of pleometrosis.

Once they have been replaced by the ☿, the fertile ♀ of large colonies, fed by their children, become scarcely more than egg-laying machines, often surrounded by a body-guard of nurses. Their ovaries grow enormously (in

Anergates atratulus, for example), and the ☿ they produce become larger and often polymorphous; they also lay ♂ and ♀ eggs. But this is not the case in various small colonies, such as those of *Leptothorax* and the primitive sub-family, *Ponerinæ*, where the ♀ remain more or less active after the foundation, and help the ☿ to carry and feed larvæ, take food on their own account, etc.; I have even seen them take an active part in the defence of the nest or in flight. Here again, all sorts of transitions can be observed.

We come now to a very different case of colony-foundation, which I myself observed more than 56 years ago. At the edge of a garden, a strong colony of *F. pratensis* began to found a second nest *B*, which was rapidly populated. In another place, the inhabitants of *A* founded almost at the same time a third nest *C* at the end of one of their other roads. But the nest *B* apparently failed after a short time to accommodate them, for they prolonged their road in the same direction, moving farther and farther away from *A*, and founded a fourth nest *D*, a long way from *B* and consequently almost double the distance from *A*. However, the ants kept up their direct relations between *A* and *D* throughout the summer, despite the considerable distance. But the winter interrupted them. In the spring of 1866, the inhabitants of *D* found a clump of trees to exploit hard by, and did not return very far in the direction of *A*. On the contrary, they went and founded a fifth nest *E* on their own account, farther away from *A*, and their colony flourished henceforth in the two nests *D* and *E*. Some ants from *A*, on the other hand, ceased to go to the nest *B*, in order to strengthen their nests *C-A*, and developed considerably without re-establishing their relations with *D-E*. In 1869, I put a handful of *A* ants near the *D* nest; a poison battle followed, and the *A* ants were put to flight.

It is evident, though I did not see it myself, that in 1865 the ants *A* had been obliged to transport to *B* a number of their fertile ♀, which afterwards passed on to *D*. However this may be, we have here a duly authenticated case of the division of a polycalic colony into two formicaries, which afterwards became antagonistic, for the individual memories of ants scarcely extend beyond their own formicary, after their winter sleep, unless direct relations are re-established between the nests immediately after. We can hardly say whether these facts are common in nature. Brun and Wasmann have observed others of a similar character; but they always concern species which make polycalic colonies. We may presume that they are frequent there, but scarcely so in other cases.

Add to this one more fact. In large polycalic formicaries, many fertile ♀ which have just mated, revert to the large domain of their own colony, in which they are amicably received or retained, and adopted. It was this more or less exceptional fact which Huber wrongly generalized, as we said before, with regard to the yearly maintenance of *all* formicaries. But it has this result among the European *F. rufa* and *exsecta* and the American *exsectoides*, etc., that single polycalic colonies may persist for more than 80 years, as I was informed in one case by Charles Darwin. My own observations on formicary *A* of the above-cited *F. pratensis* prove that they may persist for at least 56 years.

Huber has shown, by positive examples, how the worker-forms of certain ants forcibly retain some ♀ which have been fertilized by their brother ♂ in their own colony, before taking to flight.

This brings us to some curious facts which I once discovered—though I did not understand them—through happening upon some small mixed colonies (two different species mingled in perfect friendship)—in Europe, *Formica exsecta* and *pratensis* in company with *F. fusca*, *Tapinoma erraticum* with *Bothriomyrmex meridionalis*, and in the United States, *Formica exsectoides* in company with *F. subsericea*, etc. But Wheeler and Wasmann must have the credit of proving that these cases and others besides are due to a kind of parasitism in the fertile ♀. Under such circumstances, she is relatively smaller than in the species where she is capable of founding a colony unaided. But things are very different in various cases we are to examine.

The fission of polycalic colonies, their adoption of fertile ♀ of their own formicary in subsequent generations, and finally the adoption of strange fertile ♀ by a group of workers which have lost their mother or wandered too far from their nest, are so many phylogenetic devices for the compulsory adoption by a weaker species of the fertile ♀ of a stronger species. Wheeler (1904) and Viehmeyer (1908) have proved this by induction and experiment, Viehmeyer by making some *Serviformica fusca* ☿ adopt a fertile *F. truncicola* ♀, and Wheeler by making *Serviformica subsericea* ☿ of the United States adopt a fertile *F. integra* ♀. There is, nowadays, no doubt that most colonies of the European *F. truncicola*, *rufa*, *exsecta*, *pressilabris*, and the American *exsectoides*, *integra*, *ciliata*, *crinita*, *dacotensis*, *specularis*, etc., are founded by fertilized ♀ which force different races and varieties of *Serviformica fusca* to adopt them. One thing that has escaped clear observation is the manner in which the fertile ♀, if there is one, disappears from the formicary which adopts the intruder, and whether she is killed by the strange ♀ herself, immediately or later. We shall shortly see some analogies with this fact. All we can be sure of is that she disappears, that the intruder lays her eggs, which the *Serviformica* foster, that ☿, ♀ and ♂ *truncicola*, *exsecta*, etc., are hatched from them, and that the original *S. fusca*, etc., gradually disappear too. In this way most formicaries of the large *Formica rufa* and *exsecta* groups are founded, except when they arise by division or the adoption of ♀ of the same species. Wheeler has given the name 'social parasitism' to the intrusion of ♀ of *Formica rufa*, *pratensis*, *exsecta*, *integra*, etc., into the formicaries of *Serviformica fusca* in order to make them adopt their brood. This social parasitism is still *facultative*, as Brun has well pointed out. It constitutes the first stage of the parasitism of certain ants in relation to other ants. Wasmann, Brun and others have proved this by the observation of natural nests and by experiments in artificial nests. In the work from which I have already quoted, Brun gives a very good account of the matter.

But when this method of foundation is used more and more, and finally becomes the sole method, it occasions, as Wheeler has shown, a great phylogenetic diminution in the size of the ♀, so much so that they may become as small as the ☿, or even smaller, and much smaller than the ♂. This happens, for example, with *F. microgyna* and *difficilis* of the United States. I myself have found the latter, with its little yellow ♀, in the Alleghanies. *F. consocians* of the United States does likewise with *Neoformica incerta*, as Wheeler's experiments prove. The ♀ of *Aphænogaster tennesseensis*, and probably also those of *A. Mariæ*, found their colonies, so Wheeler says, in a similar manner, with the aid of the ☿ of *A. picea*, which is very common in the States.

The ♀ of our own *Dendrolasius fuliginosus*, which are relatively small, found their colonies in the same way with the aid of *Lasius umbratus* and *mixtus*, as various authors have proved, especially Crawley and Donisthorpe, who have also shown that *L. niger* adopts the fertile ♀ of *L. umbratus* and *mixtus*. By analogy, it is most probably the same with

Lasius carniolicus, which has very small ♀, but proof of this is lacking. It is true, I believe, for all the sub-genus *Oxygyna* and the genus *Cremastogaster*, and Wheeler confirms my view, though as yet we have no positive proof. These small ♀ also have curved and pointed mandibles, like the amazon ants, whereas the worker has the usual triangular dentated mandibles. Whether the ♀ uses these weapons to pierce the brains of the mothers already present in the *Cremastogaster* formicaries in which she is enforcing adoption, we shall find out if we wait long enough. In any case, the ovaries of the fertile ♀ are extremely dilated in those I have received.

In the ♀ *Bothriomyrmex*, things happen differently, and Santschi has given us clear and definite proof of the real facts. The small ♀ have the same aromatic odour as *Tapinoma erraticum* and *nigerrimum*, though their ☿ do not possess this odour. Thus protected, one of these females, as soon as she has been fertilized, enters a *Tapinoma* formicary, where she easily obtains adoption. But her first action is then the one represented in fig. 72; she seeks out the fertile *Tapinoma* ♀, climbs on to their backs, fixes her mandibles firmly into their necks, between the head and the pronotum, and thus decapitates them! Directly they perceive the dangerous intruder, the *Tapinoma* ♀ flee; and Santschi thinks they take part of the colony with them. The fertile *Bothriomyrmex* ♀ settles upon the brood and has therefore no need of many workers to help her. When this exploit is finished, she becomes sole queen of the nest, and lays eggs which are tenderly reared by the few ☿ *Tapinoma* which remained faithful to her, and by those which are hatched from the

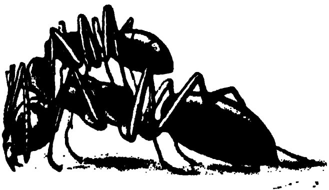


Fig. 72

nymphs, none of whom have any suspicions of the trick which this little humbug has played upon them; I was far from suspecting this in 1871, when I discovered under a stone at Stresa on Lake Maggiore, the first incipient mixed colony of *Bothriomyrnex meridionalis* and *Tapinoma erraticum.* The abdomen of the fertile *Bothriomyrmex* ♀ established in this way acquires large dimensions owing to the development of the ovaries. Thus she becomes a true idle queen, similar to those of *Anergates*, while her ☿ do all the work and gradually replace entirely those of *Tapinoma*, which die out for want of successors. Although they do not possess the *Tapinoma* odour, these ♀, whose anal glands were shown in figs. 13 and 22 (Part I), secrete in these glands a poison which is very dangerous to their enemies. Everything else happens in this case, therefore, as it does with the *Formica* of the *rufa* and *exsecta* groups, etc.

We come now to Huber's famous amazon ant, *Polyergus rufescens*, whose ♀, represented in Plate III (Part I) has curved and pointed mandibles, just as ill-suited for work as those of her idle ☿, shown at *O* in the same plate. Huber, myself and others have vainly puzzled ourselves as to how an ant so dependent upon her slaves can found a colony. In 1869 and 1872 I made two attempts to get a fertile ♀ of *P. rufescens* adopted once by workers of *Serviformica fusca* and again by those of *S. rufibarbis*. Both colonies agreed without any trouble to complete adoption, but the result of my experiment was ruined in one case by the death of the ♀, which had formerly endured the attacks of an army of her own species, and in the other by my own negligence. All credit for the successful investigation of the matter is due to Emery, whose result may be summarized as follows:

In 1908, he experimented with an artificial apparatus of the Janet type, placing in it a fertile amazon ♀ with ten

Serviformica fusca ☿ and their ♀. After 20 minutes, despite the hostility of the ☿ *fusca*, the ♀ amazon approached the ♀ *fusca* and killed her by piercing her head. But she took good care not to do the same thing to the workers, and patiently allowed them to pluck at her legs all day long, with scarcely a show of defending herself. Next day the attacks became weaker and weaker, and during the days that followed she was adopted with all honour as queen. The following spring, as late as May, she began to lay, but to a very small extent in spite of abundant food. Only seven larvæ survived and spun cocoons. Two of them, and no more, managed to hatch, but they proved to be extremely small ☿, which died in the course of the winter, together with most of the *fusca*.

In 1909 the untiring Emery repeated his experiment, but this time with some hundred *fusca* workers with a fertile female, larvæ and cocoons. The new fertile ♀ behaved like the other, killing the fertile *fusca* ♀ etc. The corpse of the ♀ was afterwards surrounded by a few ☿, then thrown away, and the amazon ♀ was adopted in her place.

Emery then put his former amazon ♀ of 1908 among the few *fusca* which remained, in the same Janet nest with the newcomer. The result was very satisfactory, although the two ♀ amazons began by quarrelling whenever they met. At this juncture, Emery noticed that in the Janet nests, with their spacious apartments, the *fusca* often succeeded in killing the amazon ♀ at the very beginning, during such attempts at adoption. In the narrow passages of the natural nests, the intruding ♀ must have much more trouble in finding and reaching the *fusca* queen or queens. On the other hand, I think the *fusca* ☿ must have much more trouble in killing the amazon ♀, for they have much less opportunity of uniting their forces here than in the Janet nests.

At the beginning of May, Emery saw some ☿ *fusca* carrying a small heap of eggs in his formicary where the two queens were living. In June the larvæ spun cocoons and in July the first ☿ were hatched. But strange to say, they were not treated amicably by the *fusca* ☿, which pulled their legs and antennæ. The amazons remained passive, without reacting, and two days later, when a number of others were hatched, all discord ceased. By the end of the autumn 50-60 amazons of small size had become adult.

During the first year of an amazon formicary, Emery tells us, the relations between the amazons and the *fusca* are different from what they are later on. The *fusca*, which are the so-called slaves, are much more like the real managers or teachers of the colony. They do not allow an amazon to block up the lighted portions of the nest; when she does so, they draw her away by the mandibles to the dark part; in short, they treat the amazons like myrmecophilic guests. Emery does not think that a colony of amazons which begins in this way goes out slave-raiding during the first two years of its existence. During the first year, the queen is introduced, kills the *fusca* ♀ and enforces adoption; this is the period of infancy. The second year, ☿ are hatched and learn their duties; this is youth. The third year is adolescence.

In August, 1911, Emery constructed a plaster arena on my old system, and attached to it two tubes, one open, communicating with his Janet nest, which contained the mixed amazon-*fusca* colony of 1908-1910, the other closed, leading to another Janet nest which was populated by ten strange ☿ *fusca* from a natural colony and their cocoons. The amazon-*fusca* advanced into the arena. Only the next day, Emery opened the tube of the nest containing pure *fusca*, and watched them. After some time, a ☿ amazon penetrated into the *fusca* nest and produced a general state of panic. She snatched up a cocoon and carried it to her formicary. Then, without any warning to her companions, she returned alone, about ten times in succession, bearing each time a cocoon.

Emery then carried his amazon nest several times out into the fields, allowing the ants to come out when they pleased. He observed that isolated ☿ amazons, which came forth and encountered *S. fusca* or *rufibarbis* nests with open doors, forced their way in alone with a most foolhardy courage. Sometimes, however, they succeeded in returning to their formicary. In any case, the amazon ☿ which came out alone during the warm summer days did not return until some time afterwards. Emery cannot certify that all the exploring ☿ which served later on as guides in the expedition had previously penetrated a nest of the auxiliary (slave) species which they discovered. But after observing several expeditions from his artificial formicary, he reached the conviction that the exploratory exercises of the amazon ☿ which went out alone were definitely intended to enable them afterwards to guide their companions in expeditions during the summer, wherever there was any hope of a good harvest. Emery thus gave us experimental confirmation of the opinion advanced by Huber in 1810 and by myself in 1874, on the subject of these individual explorations by amazon ☿ in natural formicaries.

Thanks to Emery's perseverance for three or four years, the outstanding difficulty in connection with the foundation of *Polyergus rufescens* colonies has thus been completely elucidated in all its stages. The above facts are extraordinarily instructive. They also show progressive individual adaptation—I had almost said progressive tradition—in the *Serviformica fusca* of mixed colonies to the predatory instinct of the amazons.

This brings us to the foundation of other colonies of slave-making species. We are indebted to Wheeler (1905-1906) for having elucidated the matter in connection with *Raptiformica sanguinea* and its races. He placed a virgin ♀ of *R. sanguinea-rubicunda* (United States) near 33 ☿, 150 cocoons and a few *S. fusca-subsericea* larvæ, which were in the dark chamber of his apparatus. The ☿ seized some cocoons and fled into the light chambers; one or two of them attacked the ♀, who shook them off and killed one of them. Several *subsericea* workers then stole into the dark chamber to secure cocoons and carry them to the remotest corner of the light chamber. At the end of the morning, the ♀ became more and more excited; she killed five more ☿ and was busy carrying the cocoons back from the illuminated into the dark chamber, where she had already stored most of them in a corner. In a few minutes she had secured all the cocoons in the light chamber, thirty-six in all. She interrupted her task twice only, each time to kill a *subsericea* ☿ that came within her reach. She then made a compact pile of the cocoons, and on perceiving two *subsericea* ☿ which had persisted in recapturing a cocoon, she promptly killed them. All this resembled a miniature slave raid, conducted by a single ♀; the executions were as ruthless as those of the *sanguinea* ♀, but neater, swifter and surer, in accordance with the large size of the ♀.

Next day only two *subsericea* ☿ survived, and had re-captured thirty of their cocoons. By half-past ten the ♀ had entered the light chamber room and re-captured all but six of the cocoons. The two ☿ had lost heart. At half-past eleven one of them entered the dark chamber, but was driven out by the *rubicunda* ♀, which had not forgotten the six remaining cocoons, but went back and re-captured four at noon. She went in search of the last but one at about one o'clock, threatening with her mandibles everything that seemed hostile. By July 10th she had killed the last two *subsericea* ☿

and taken the last cocoon to the dark chamber. Henceforth she defended the cocoons and larvæ energetically, biting Wheeler's finger. By July 16th, five *subsericea* callow workers had come out of their cocoons, and Wheeler saw the *rubicunda* ♀ proceeding with this operation herself, opening the cocoon by making an elliptical hole in it with her mandibles. The ♀ then devoured one of the larvæ. Thereafter a host of cocoons were opened in the same way, and the *subsericea* callows began to give the ♀ so much help in her work that by July 24th, 130 ☿ were hatched. The ♀ thereupon changed her tactics; she ceased to be aggressive, allowed herself to be fed and fled into darkness at the first sign of danger. Wheeler concluded his experiment on July 26th.

At first he was unfavourably criticized on the grounds that his ♀ was a virgin. But Viehmeyer and Wasmann repeated the experiment with some European *F. sanguinea*, Wheeler himself doing the same with the *aserva* and *subintegra* races of the United States, and the results were identical with those obtained from the virgin *rubicunda* ♀. No doubt can therefore remain. The fertile ♀ of *Raptiformica sanguinea* and its races founds her colony by making a solitary attack upon a small colony of the *Serviformica fusca* group and the *rufibarbis* races, etc., whose inhabitants she puts to flight and kills in order to steal their cocoons.

In 1909 I discovered at Valais, in the presence of Wheeler, Viehmeyer and others, an incipient colony consisting of two fertile *R. sanguinea* ♀, living together in the middle of a small heap of *S. rufibarbis* cocoons and nymphs and three or four young ☿ of this latter species, which had evidently been stolen. But this incipient formicary also contained some ten minor *sanguinea* workers, like those belonging to colonies founded by a fertile female alone, although fairly adult.

Here we may wonder whether we are faced with an exceptional state of affairs or whether one at least of the two ♀ had reared her brood alone before attacking a small *S. rufibarbis* colony. I am content to ask the question, without supplying an answer. Wasmann thinks that this may have been an old and decadent formicary; I am persuaded that under the circumstances in which these ants were found, such a theory is inadmissible.

I once proved that ♀ ants of different species or races sometimes unite with others to found a colony. This condition has been called by Wasmann *allometrosis*. One day in August, for example, Viehmeyer found in an underground chamber a fertile *R. sanguinea* ♀ with two very small *sanguinea* ☿, two or three *fusca*, and side by side with the rest a fertile *S. fusca* female with two small ☿ and a small cocoon of the same species. When placed in a Lubbock nest, the two groups separated from each other. Here Wasmann allows allometrosis.

Wasmann gives us the following summary of the various somewhat exceptional methods by which *R. sanguinea* and its races found their colonies without making a solitary attack upon a formicary of the slave-species:

(1) Foundation of polycalic colonies without slaves, the native fertile ♀ being retained in their own domain (r. *aserva* of America, and my colony from the Boverat chalet, of which we shall speak in Part IV., Ch VII, 1*a*).

(2) Adoption of fertile ♀ by *sanguinea* ☿ from strange formicaries.

(3) Adoption of fertile *sanguinea* ♀ by natural colonies of one of the slave species.

(4) A fertile *sanguinea* ♀ discovers and rears some cocoons which had been forgotten in the recently plundered and abandoned nest of a slave-species.

(5) A fertile *sanguinea* ♀ established an alliance, after her nuptial flight, with a fertile ♀ of the slave species. In this case, demonstrated by Viehmeyer, the *sanguinea* ♀ allows the slave ♀ to hatch and rear her first offspring, and ends by killing her or driving her away.

Whatever happens, one thing is certain, the procedure of the *Raptiformica* ♀ in the foundation of their colony appears to vary, and is fundamentally different, in short, from that of *Polyergus*. As this ant cannot feed herself, she gets the ☿ to adopt her in a more dependent fashion, contenting herself with killing the ♀ which might compete with her egg-laying. The *Raptiformica* ♀ are much more active in their ordinary insolent attacks, which are conducted alone in a manner as impudent as it is courageous.

It is to Adlerz that we are indebted for having elucidated the habits of that curious ant, *Harpagoxenus sublevis*, which is the parasitic or rather slave-making guest of other ants, *Leptothorax* (*Mychothorax*) *acervorum* and *muscorum*. *Harpagoxenus* had a kind of ergatogyne worker, represented in fig. 73, which takes advantage of her size and her hard chitinous covering to break roughly, either alone or with several companions, into a colony of the above-mentioned peaceful *Leptothorax*, drive them from their nest, monopolize their young of all sexes, and rear them as auxiliaries to rear and feed her own progeny. At the same time, this creature has a winged ♀ and ♂, and is able to eat and work unaided. Her American equivalent, *H. americanus*, is still more degenerate and dependent, and acts in much the same manner towards *L. curvispinosus* and

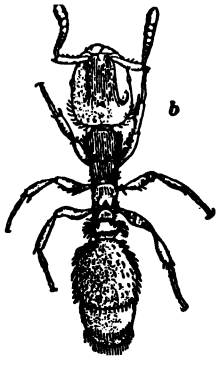


Fig. 73

longispinosus. We shall deal with both of them again in Part IV.

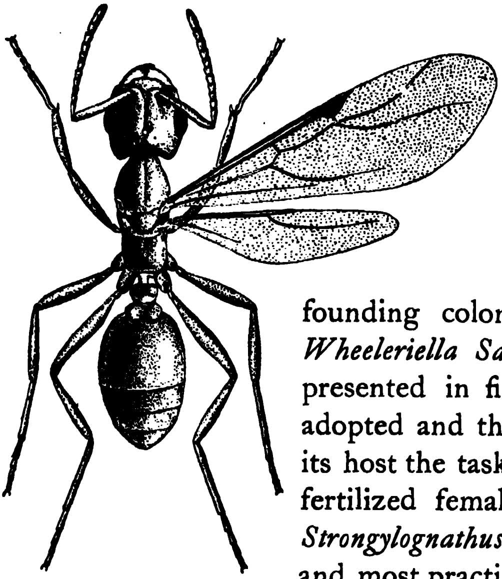


Fig. 74

Other species of parasites, of which we shall speak in Chapter VII, have yet other methods of founding colonies. One of these, *Wheeleriella Santschii*, which is represented in fig. 74, gets herself adopted and then leaves to the ☿ of its host the task of killing their own fertilized female. Others, certain *Strongylognathus*, have the simplest and most practical system of all, beginning in a peaceful manner 'before the egg.' After mating, their little female is no sooner fertilized and deprived of her wings than she walks about the ground seeking for a large ♀, likewise fertilized, and belonging to her host, *Tetramorium cæspitum.* As the aerial nuptials of the two ants take place at the same time and as *T. cæspitum* is extremely common, she succeeds without much trouble. After this she will not leave the host ♀, but lives with her in the hermit-chamber built under the earth by her active companion, and shares her fast. It was Wasmann who discovered these facts in connection with *S. testaceus.* Mrazek confirmed the matter in July by an experiment in an artificial nest, where the fertile ants of the two species lived peaceably together as recluses. The *Tetramorium* ♀ was evidently the first to lay and to rear her hard-working little ☿; but the two ♀ died in November, before the first ☿ were hatched. From the first, the two ♀ lived in perfect harmony, as they did later on in the same formicary, where the *Tetramorium* ☿, in their innocence, were much fonder of rearing the parasitic ♀ and ♂ than those of their own mother. These ants were much larger and required more food. On the other hand, they reared a host of ☿ larvæ of their own species, which continued in the same way, without suspecting that they were being befooled all their lives. The ♀ and winged ♂ of *T. cæspitum* are very seldom found in a mixed colony of *S. testaceus.*

You see, dear reader, what a wide variety there is in the instinctive methods by which the foundation of new colonies has been adapted to various circumstances in natural phylogeny. So many things can happen in millions of years!

But we have still to remember one point. As we have seen, parthenogenesis of ☿, that is, their faculty of laying eggs without being fertilized, has been proved, first by myself and then by Reichenbach in 1902. I had supposed that the ☿, like those of the bees, could only lay ♂ eggs; Reichenbach showed that *Lasius* sometimes lays ☿ eggs. Nevertheless, numerous facts seem to prove that a formicary which no longer has a fertilized ♀, or at least a fertilized ergatogyne, is gradually extinguished if it does not obtain another by adoption. Parthenogenesis, even that of workers, appears therefore to serve only as a stop-gap measure. Indeed it is not likely that nature, otherwise so economical in her living forces, should maintain so complicated an apparatus for the foundation of a formicary as that described above, if the conservation of formicaries could be achieved by simple parthenogenesis. Why should there be so many idle and imbecile ♂, if they were in no way necessary? This question implies its own answer.

We have mentioned *Formica rufa* and *pratensis* formicaries lasting 80 and 55 years. Others only last a few years, but in the end they are all exterminated, usually in consequence of the loss of their fertile ♀, whether they keep one or several. We have also seen that the fertility of the ♀ continues only so long as their seminal vesicles still contain sperm. Only the formicaries capable of renewing themselves constantly by the adoption of new fertile ♀ can last for a number of years, and this is exactly what happens with *F. rufa*, *pratensis*, *exsecta*, etc.

Chapter III

ANT-LIFE INSIDE THE NEST

In this domain, yet once more, Huber was our pioneer. But since his time, the perfecting of artificial apparatus has enabled Janet to display even the interior life of ants to the public which visits any Exhibition.

Let us begin by stating that only adult ants possess antennæ and eyes, which means that as they alone are capable of seeing and perceiving by topochemical smell, they alone are also capable of distinguishing the inhabitants of their formicary one from another, whereas the larvæ and nymphs are not. The guests involve another problem altogether; I have referred to it in Part II, and do not intend to do so again. Some of them doubtless know the formicary where they obtain shelter by trickery, but we have no more concern with them here. And since the ♂ and virgin ♀ do nothing or practically nothing, and the fertile ♀, after the foundation, do nothing but lay eggs, it follows that the ☿ alone, together with the soldiers, when there are such, are the true queens of the formicaries, as hard-working communists. Work, not marriage and debauchery, which are the sole ideal of so many human beings, is at once their province and their pleasure.

1 Rest. When we see ants outside their nest, we always find them moving—running, even, at varying paces, some slowly, some in abrupt spurts, interrupted by sudden

pauses, while others ferret about to right and to left, and others again go as straight as an arrow. Many of them are laden with heavy prey, or still heavier building materials, others with companions or larvæ which they are carrying away, while some are returning with a cropful of honeydew; not one merely abandons herself to *dolce far niente*. And in warm weather, as we have seen, work does not cease at night. It seems surprising that their little organisms should be able to resist so much strain.

Observations in the nests designed by Huber, Lubbock or Janet show us how this happens. Ants do not work all the time; they rest in between whiles. When one of them comes back from a long journey with a cropful of honey-dew, her companions assail her first of all to obtain regurgitation, which gives her the pleasure of re-tasting the juices. They next help her with her toilet. Finally, when she is quite clean, she retires quietly to the corner of the nest with other ants which are resting, and goes to sleep along with them. It is difficult to say whether this is a true sleep. In any case, ants which are resting do not like to be disturbed.

When some kill-joy recruiter arrives, or some danger threatening the formicary is announced, the sleeper begins by turning a deaf ear, or rather a deaf antenna; first of all she tries to show no reaction, as though she did not understand. But if the recruiter insists or the general alarm becomes urgent, she is obliged to rouse herself. Nothing is more comical than to watch an ant, beautifully clean and shiny, being disturbed in her rest. At first she is only half-wakened as though in a stupefying doze, and her movements are slow and lazy. When all that is asked of her is to allow herself to be carried by a recruiter, well and good; but not so when it is a case of fighting or fleeing. A battle can certainly awaken ants very quickly; but in flight, especially when demanded by a sudden, irresistible attack, I have often seen ☿ betray their half-slumbering condition by their slackness, by a certain cowardice and by the abandonment of their larvæ and nymphs in the course of their flight. In such cases, a general discouragement mingles with the startled feelings of ants which have been suddenly awakened and have not had time to recover themselves. These may be recognized by their shiny appearance and their slow gait, which renders them more or less distinguishable from those which were awake and active at the moment of attack. In a word, ants rest after their work, as we do.

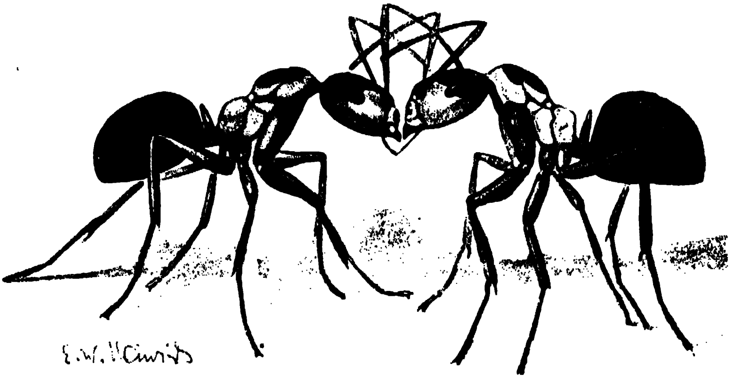


Fig. 75

2 Language. Huber was the discoverer of the antennal language of ants, without knowing that the antennæ were their organs of smell. In Chapter II, Part II (Physiology and Psychology) we have already explained this antennal ant-language and the head-blows which are sometimes associated with it. This is the way in which they transmit to their companions their feelings, their discoveries, their anxieties, their intentions, with the aid of signs whose enumeration we have taken from Wasmann. Fig. 75 represents two ants talking to each other, in so far as a motionless

figure can enable movements to be appreciated. Imagine these two ants, dear reader, alive and on a small scale, and you will have the reality before your eyes. You will then see their antennæ alternating in rapid movements, conveying from one to the other their topochemical sensations. But what can they tell each other in this way? Here we must learn to hold our tongues and, at most, accept Wasmann's summary indications (given in Part II), however much we may be tempted to humanize the thoughts of ants. We must take care not to indulge in romance. Nevertheless, dear reader, if you really want a romance, I specially recommend you that of Han Ryner, *L'Homme fourmi* (The Ant Man), Paris, 1901, in which you will read the story of a man whom a fairy transforms into an ant for a year. The author seems to be well acquainted with the habits of ants; in any case, when his hero becomes a man again, he regretfully recalls the time when he was an ant with a dear companion whom he called 'Aristotle.'

I will now allow Huber to speak of some ants which he had frightened in one of his artificial nests. "One day when they were gathered at the bottom of the apparatus and occupied in licking up drops of water trickling in between the wood-fibres, which they found preferable to drinking out of the little basin, I amused myself by disturbing them; this little experiment brought about a scene which seemed to me conclusive. The majority of the ants at once climbed along the bottom of the apparatus, though there still remained a small number which showed no signs of alarm at my presence, and which went on drinking. But one of the first came down again and proceeded to approach a companion, who appeared to be absorbed in the pleasure of quenching her thirst; she pushed this ant several times with her mandibles, lifting her head up and down in a jerky fashion, and soon succeeded in getting her to move away; this officious ant then turned her attention to another worker which was still drinking, and tried to arouse her by going behind her and striking her abdomen; but seeing that she did not seem to understand, the herald of danger came nearer and gave her two or three blows with the tips of her jaws; aware at last that it was necessary to move off, the ant ran hurriedly up beneath the bell-jar; a third companion, warned in the same manner by the same ant, promptly betook herself into shelter; but a fourth, which remained alone at the edge of the water, did not withdraw, despite all proofs of solicitude. She appeared to pay no attention to the reiterated shocks given her by her counsellor,

Fig. 76

which finally grasped her by one of her hind legs and pulled her sharply; the ant which was slaking her thirst turned round at last, opening her large pincers with every sign of anger, and then began quietly to drink again. However, her companion left her no time to do this, but passed in front of her, seized her by the mandibles and dragged her swiftly into the nest."

Certainly, the more I think about it, the more clearly I see that there are incontestable advantages about topochemical antennal language—mimetic, quick, silent, sure and expressive—over our redundant and often lying oral verbiage, with its big words which lead us into error almost more frequently than they help us to understand the truth! In the nest, when ants are once awakened from their rest, they scarcely speak to each other at all except to beg a newcomer for honey-dew, as shown in figs. 76 and 79; they have something better to do. Fig. 76, after Miss Fielde, shows a mixed colony consisting of three different genera and even two different sub-families, living and talking together in peace.

3 Brood. Fig. 77, after André, represents approximately the division of the brood in a *Lasius* nest; the eggs are at the top; then come the larvæ, classified according to size, and finally the cocoons at the bottom. This is sometimes more or less the case; but the somewhat pedantic regularity shown in the drawing is exceptional. Often enough cocoons, nymphs, larvæ of all sizes and even eggs can be seen heaped together in one chamber. Nevertheless, a certain division in an order analogous to that of our figure is fairly common, even in a horizontal arrangement—under a single stone, for instance.

According to Janet, the fertilized ♀ (sometimes also a ☿) which is laying an egg lowers her head and thorax, raises her abdomen and thrusts out her sting, when she has one. The egg then appears. In some cases, so Wheeler and Viehmeyer tell us, the ☿ which are watching the laying process help to extract the egg, which they immediately carry away. At other times, the female squeezes it out by rubbing the end of her abdomen against the earth; young fertile ♀ even manage this by applying their curved mandibles to their abdomens. While the eggs are being laid, a bodyguard of workers surrounds the ♀ and licks her, especially on the abdomen, which they feel with their antennæ. Viehmeyer saw one *R.** *sanguinea* ♀ laying at the rate of one egg every ten minutes or so. The intervals vary a great deal according to the species.

Fig. 77

Von Buttel says that as soon as the eggs are laid they show inequalities in

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* I beg the reader's indulgence for using as an abbreviation for the sub-genera *Raptiformica* (*sanguinea* and its races) and *Serviformica* (*fusca*, *rufibarbis*, *cinerea*), sometimes the letters *R.* and *S.*, and sometimes the letter of the genus *Formica*, which is common to them: *F.*

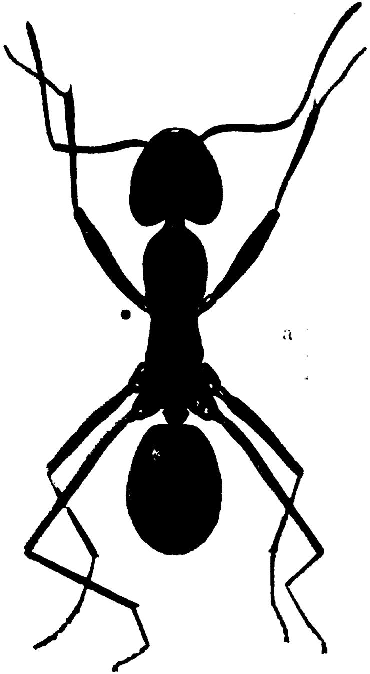
size, and this, in my opinion, probably depends upon the future polymorphism, in other words, the future size of the individuals which are to come out of them. But besides this, Huber had already proved carefully that the white, milky egg grows after it is laid; it becomes yellowish and transparent, and then slightly curved, before it opens and gives birth to the larva. As they are constantly being licked by the ☿, their growth is evidently due to the saliva, acting by endosmosis, that is, by filtration of the secretion through the skin (outer membrane) of the egg. Wheeler says that certain ants (*Cerapachys*, *Eciton*) even hatch their eggs by sitting on them. In summer, the egg stage lasts from one to five weeks; in other species, however, it lasts throughout the winter. The ☿ devour a great many eggs, and even the fertile ♀, as we have seen, devour a number of those which they lay themselves; Viehmeyer has seen egg-laying workers curl up their own abdomens and there and then devour the eggs which emerged. In justification of the ants, I beg some of my women readers to avoid the mistaken notion that these eggs are to be compared with their own little children or the embryos which precede them.

We have described the larvæ in Part I. In the *Ponerinæ*, they themselves eat the fragments of prey which are brought them by the ☿. In the other sub-families, (though we have little evidence as to the *Dorylinæ*) the ☿ cram them in the manner described in Chapter IV, Part II, in connection with the *Lomechusa*. The ant alone is active; she slowly disgorges the meat or honey-dew into the mouth of the larva, which merely swallows it, whereas among adult ants (see the figure on the cover) it is the soliciting ant which actively licks up the drop disgorged by her motionless companion. But those larvæ which have mobile heads (*Lasius*, *Formica*, *Myrmica*, etc.) can ask for food by moving

a. *Iridomyrmex detectus* var. *viridiænea* ☿. Australia. 7·9 mm.

b. *Dolichoderus* (*Hypoclinea*) *Doriæ* r. *extensispinosus* ☿. Australia. 8 mm.

c. *Myrmoteras Binghami* ☿. Burma. 5 mm.



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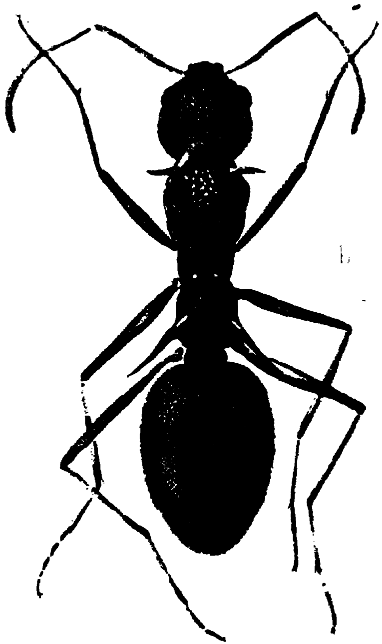

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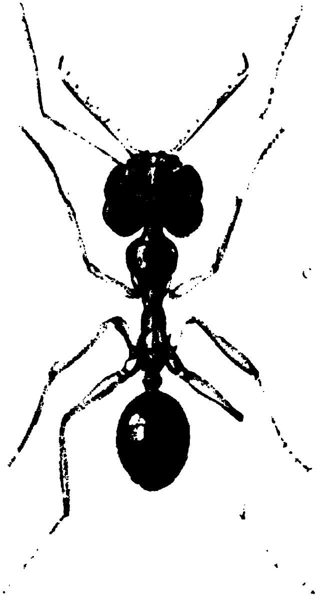

c

their heads. We should try to imagine the enormous amount of work which the care of the larvæ inflicts upon the ☿: continual regurgitation to these ravenous creatures, perpetual cleansing (of the eggs too!) with the tongue and mandibles, transport from one corner of the nest to the other every moment, in accordance with the temperature. We shall then understand why it is that so many workers have to invade trees, hillocks or enemies, either to milk aphids or to look for prey—and we shall excuse the ants for taking some rest!

This is what Huber has to say about the matter: "As soon as the ants were warned that the sun's rays were about to appear, they became busy with their larvæ and nymphs; they bore them in great haste to the top of the formicary, where they left them for a time exposed to the influence of the heat. Their ardour did not slacken; the female larvæ, much larger and heavier than those of the other castes, were borne with a certain amount of difficulty through the narrow passages leading from the interior of the formicary to the exterior and placed in the sun side by side with those of the workers and males; when they had been there a quarter of an hour, the ants took them away and placed them under shelter from the direct rays, in compartments intended for them, under a layer of thatch which did not entirely intercept the heat."

When the larva is transformed into a nymph, with or without a cocoon, the ☿ continue to lavish upon them every care in the way of cleansing operations and transport in view of temperature; feeding alone ceases. We have already seen how they supply fragments of earth to the larva which is about to make a cocoon, wherewith to attach its first threads, how they afterwards clean the cocoon, how they cut the shell in an irreproachable manner with the teeth of their mandibles before hatching takes place, and finally how they sometimes even help the newly-hatched ant to come out of the skin and spread its wings.

I will quote Huber once more: "A sort of ferment prevailed in this part of the formicary. A number of ants, busied in releasing the winged creature from its bonds, rested or rose in turn, and came back hurriedly to aid their companions in this enterprise, so that they were soon able to bring it out of its prison; one raised the cut band all the way along the shell, while others drew the ant gently from its natal resting-place. At last I saw it come out; it could neither fly nor walk, and could scarcely stand upright on its legs, for it was still swathed in its last membrane, and unable to cast it off of its own accord. The workers had no thought of abandoning it in this new quandary; they stripped it of the silky pellicle in which all parts of its body were clothed, drew the antennæ and the palpi tenderly from their sheath, then unfastened the legs and wings and released the body, the abdomen and its pedicel from their covering."

With the care of the brood is to be ranked that which a special bodyguard of workers give their fertile ♀. Huber gives an excellent description of these in connection with *Lasius flavùs*, for instance, whose ☿ often cover the female with their bodies, and never cease to caress her, feed her, lead her to the most propitious temperature, lick her and keep her clean, gathering up meanwhile every egg that she lays.

4 Alarm. Directly the ☿ which are guarding the doors of the nest perceive a danger, especially the presence of an enemy species, they rush to the interior of the nest and give the alarm to the others in their antennal language, and also by blows with the head or mandibles. Some of them then hurry out to the defence, while others carry the brood to the very bottom of the nest before they also go to lend their aid. The ♂ and ♀ alike flee to the bottom of the subterranean

galleries. All this takes place in a flash; it can be observed very well in artificial apparatus through glass. At such a time we have reason to admire the effects of the antennal language signs, and their repercussion on the various feelings of anger and fear which affect our little friends! We have just seen this in the above quotation from Huber with regard to antennal language.

5 Toilet. Here we must be careful to distinguish between the individual toilet which each ant performs with its own limbs, more especially with its precious antennæ, aided by the comb on its spur and the brush on its anterior tarsi (see fig. 78), and the social toilet with which it gratifies its ☿, ♀ and ♂ companions. The second kind, as we have seen, is achieved with the tongue and mandibles. It must not be forgotten that even the slenderest ☿ is incapable of cleaning its own head and thorax when they are covered with earth or other dirt. For this purpose, therefore, it is obliged to have recourse to its companions which undertake the task on its return home, from either a fight or an expedition in search of honey-dew. We have seen that they proceed in a similar manner with their eggs, larvæ, nymphs and cocoons. Ants have a horror of dirt, which is yet another way in which they put many human beings to shame.

Fig. 78

In 1889 (*Notes of Indian Ants*), James Rothney described *Diacamma vagans*, one of the *Ponerinæ* which he had specially selected for observation at Barrackpore in India.

On the stones at the entrance to a passage extending underneath a road, in the shade of the forest, he says that at any time of the year, but especially in warm and rainy weather, a number of *Diacamma vagans* ☿ will pair off in order to perform what he calls their mutual toilet. Two ants place themselves face to face with each other, rubbing and caressing each other with their antennæ, first advancing then retiring a little. After this, one jumps lightly on to the other's back and catches hold of her tenderly by the mandibles. The antennal caresses are renewed and the legs are

Fig. 79

also employed in the same manner; finally the mandibles are made to glide gently, in alternating rhythm, along the limbs of the other ☿. During this operation the ant so treated beats time with its antennæ and stretches its legs in its enjoyment of the delicious sensation of being combed and cleaned. There can be no doubt that the two ants take great pleasure in this mutual play, which can be observed in all its stages. It sometimes varies a little—three ants, according to Rothney, may take part in it instead of two, or one of those which are to be combed may affect a kind of timid resistance.

6 Mutual Regurgitation. We have already pointed out the difference between the ants' manner of feeding their larvæ and guests and that of their mutual regurgitation of honey-dew, which can be seen in the figure on the cover and in fig. 79. The ant which is regurgitating remains quiet, with open mandibles and antennæ held back, while the one that is soliciting caresses her forehead with her own antennæ and swallows the regurgitated drop by closing her mandibles. I shall not refer to this again. The *Ponerinæ* scarcely appear to carry on mutual regurgitation at all, being almost entirely carnivorous. However, we are still sadly in need of a thorough investigation of the habits of the great tropical *Ponerinæ*.

7 Nurses. In steppes and many deserts, in Australia, Mexico, the United States, South Africa, etc., certain ants have singular habits adapted to the terrible seasonal droughts. Instead of making deep and spacious underground granaries, as *Messor* does in the Sahara, they replace them by living bottles to supply them with food-provisions during the dry seasons, having previously hastened to take advantage of the rain to fill their bottles with honey-dew extracted from gall-nuts, aphids or their other domestic animals, of which we shall speak of in Chapter V.

These bottles, which have been called 'nurses,' are simply the large ☿ of the species, and sometimes also the small ones, whose crops are enormous and capable of an alarming increase, such as you may see represented in figs. 80, 81 and 82, which are by no means exaggerated. In reality they are even larger. Fig. 80 shows us, in the natural size, a large chamber in the nest of *Myrmecocystus hortus-deorum* of the United States, the ceiling of which is covered with about fifty 'nurses,' hanging to it like so many provision-bottles. An ordinary ☿ is caressing them. About the year 1877, I myself received some 'nurses' like this from McCook, who had observed them in their native place, and I was then able to guarantee that their intestinal canal had not been broken, as certain writers had imagined, but simply pressed by the excessively distended crop against the wall of the abdomen, as fig. 81 shows clearly in connection with *M. melliger*. *A* shows the rectum, passing into the opening of the cloaca; *B* the stomach; *C* the

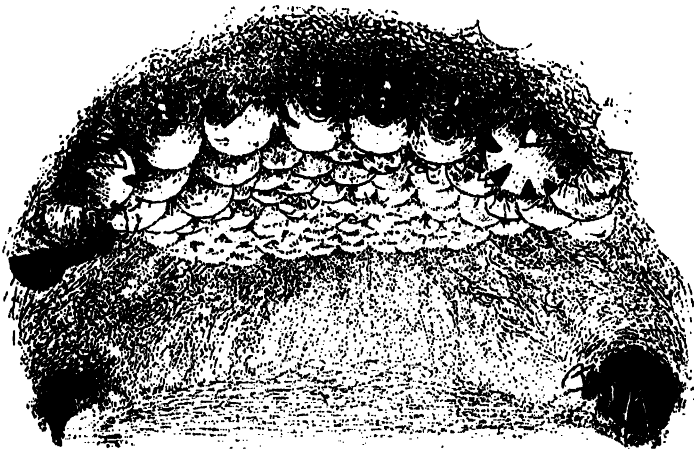

Fig. 80

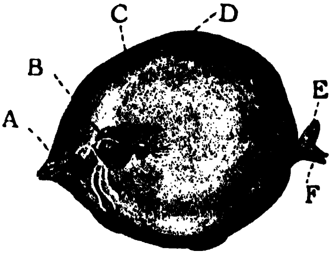

Fig. 81

crop, distended and applied to the intersegmentary wall of the abdomen; *D* the third segment of the abdomen; *E* the scale of the petiole. In front of *B* we see the gizzard with its sepals apart, and the crop swelling out between them. Finally, fig. 82, after McCook, shows us how a nurse disgorges honey-dew to three of her companions. This figure, I may mention, is not very natural, for regurgitation of this sort does not take place in the open air, but in the nest, and the antennæ of the regurgitating ant ought to be set back; on the other hand, I can guarantee the accuracy of fig. 81, save that the artist has forgotten the small fifth abdominal segment.

Fig. 82

Wheeler has succeeded in making nurses on his own account by artificial cramming with maple syrup and cane sugar, especially in the case of major *M. hortus-deorum* ☿, when still young. In 4-6 weeks he transformed them into semi-repletes, and some of them even into perfect repletes and definitive nurses. But as a result of his experiments he does not think that such a transformation can be effected when the ☿ are already adult. *M. hortus-deorum* lives at Manitou in Colorado, where it feeds chiefly on the secretion in the small galls which the Cynipid *Holcaspis perniciosus* makes on an American shinoak, *Quercus undulata*. During the night, these galls exude minute drops of a sweet liquid, and McCook observed the *Myrmecocystus* imbibing large numbers of these drops, even by night—for this ant has nocturnal habits. On returning to the nest they cram the nurses with this product, stored provisionally in their own crops.

Wheeler furthermore emphasizes the fact that the large chambers of *M. hortus-deorum*, seen in fig. 80, which are 7-10 cm. broad by 4 high at the top, are always built in extremely hard earth, at a depth of 20-25 cm. This ant's nests, according to Wheeler and McCook, are situated only on the summits of dry, stony ridges. Their galleries are spacious and well-aired, reached by a simple crater. Wheeler thinks that the purpose of this habitat is to prevent the nurse-chambers crumbling away under the influence of rain; in a word, to keep them permanently dry. This reminds me that among the larvæ of *Camponotus* (*Myrmoturba*) *Atlantis* in Algeria, which is of a somewhat pale yellow like *M. hortus-deorum*, and seems therefore to possess similar nocturnal habits, I have on many occasions found semi-nurses, swollen and differentiated, to a much less extent, it is true, than those of *Myrmecocystus*, but for the most part fairly typical. Now my observations have shown me that *C. Atlantis* also builds its nest at the top of arid, dry hills and mounds, near Batna in Souk-Arrhas, etc. Hence I suppose it must milk its cattle and gather its honey-dew at night, as *M. hortus-deorum* does, in order to cram its semi-nurses. But we must beware of generalizations. Other nurse-forming ants work by day.

Semi-nurses of this kind, similar to those of *C. Atlantis* and still capable of walking unaided, albeit in a ponderous fashion, are to be found among various ant-genera—for example, *Prenolepis imparis* of the United States, various species of *Brachymyrmex* and of the Australian *Melophorus*, *Acantholepis abdominalis* of Abyssinia, *Plagiolepis Jouberti* from the Cape of Good Hope, etc.—the nurses of this last being fairly distinct and more or less ergatogyne.

But other species show all possible transitions between semi-nurses and complete nurses, for example, *Leptomyrmex varians* of Australia, which belongs to the sub-family of *Dolichoderinæ*, and *Camponotus* (*Myrmophyma*) *inflata*, also of Australia. The nurses of *C. inflata*, which lives in deep nests under the sand, are incapable of feeding themselves, and these, like *Myrmecocystus melliger*, of Mexico, are much sought after by the natives as a dainty article of diet. The nurses of *Plagiolepis Trimeni* of the Cape have a slightly ergatoid appearance (less than those of *Pl. Jouberti*), but they are just as much swollen as those of *Myrmecocystus* and cannot walk.

As we see, nurses are formed by convergence in very disparate genera of two sub-families, by adaptation to arid, parched regions, in which rain is rare.

In passing, I must mention *Physocrema*, a sub-genus of *Cremastogaster*, whose species *inflata* and *deformis* are found in Burma and the Sunda Islands, and *arcuata* and *Montezumia* in tropical America. They are distinguished by the extreme distension of the epinotum, resulting from the hypertrophy of the metathoracic gland. Bingham has watched a sweet fluid trickling from the opening of the gland; he saw the workers of the Indian species vigorously licking one another's thoraces. That is practically all we know about this subject, which still has some surprises in store for us. I must, however, remind my readers of Chapter IV, Part II, in which they will see how that mosquito rogue, *Harpagomyia splendens*, exploits this same *Physocrema deformis* by stealing drops of honey from it. It may be that he also licks its epinotum.

8 PÆDALGUS TERMITOLESTES AND PACHYSIMA. We find in the Belgian Congo the larva of a *Pædalgus* belonging to the tribe of *Pheidologetini*, a murderous parasite of the termites, described by Wheeler in 1918. When dissected by our author, this larva proved to possess enormous salivary glands, even in its early stages, though it does not always spin any sort of cocoon. The reader will be able later on to compare figs. 133*A* and 133*B* of Part V, which, though concerned with the glands secreting the larval silk, furnish a striking analogy with the case in point. The glands of *Pædalgus* are filled with a clear liquid, whose use can only be guessed at. The *Pædalgus* ☿ feed their larvæ from mouth to mouth with honey-dew taken from the termites, which they devour. Hence Wheeler supposes that here we have another food-reservoir at the service of the ☿ of the formicary, analogous to that which the nurses provide in their crops, but chemically modified by *metabolism*, that is, by a mutual exchange of nutrition between the larvæ and their guardian for a purpose not yet clear. The system of mutual exchanges, such as those provided by *Pædalgus* and the nurses, has been described by Wheeler as *Trophallaxis.* With these ants he classes the young *Pachysima* larvæ, which have a sort of exudation rising from special tubercles, and he thinks that these tubercles represent a kind of primitive ductless gland, which achieves by simple filtration

(endosmosis) chemical exchanges between the blood, fat, etc., and also serves for mutual nutrition, by exchange with the workers. In the adult *Pachysima* larva, the exsudatory organs are atrophied. We shall return to these questions in Chapter V.

9 Migration and Transport. When a colony has been pillaged by wood-peckers, invaded by moss, disturbed by man, etc., and wishes to change its habitation, the ☿ seek a more propitious place whither all may migrate, the large species sometimes choosing a site a very long way off. The blind or subterranean species often emigrate by way of subterranean passages. The species with a good sense of smell follow each other's tracks and carry only their brood, their ♂ and sometimes their ♀ to the new abode. The worker who has found a new site, always goes in search of her companions in some way or other, according to the special development of her sense-organs, to lead them thither. Then they come back to the nest and lead others away, and so on; the winged sexes, the guests, the parasites and the brood keep close behind, whether they are carried or left to themselves. A removal like this may be effected in a very few hours, as in the case of *Tapinoma erraticum*, or last for several days. Certain ants, such as *Tapinoma* and *Dorylinæ*, are continually migrating; others, such as *Formica rufa* and *Camponotus herculeanus*, may dwell for a number of years in the same nest.

But it frequently happens that two or several ☿ discover each a different place suitable for immigration. Then follows a curious state of disorder—ants wandering to and fro and companions and dependants being carried or led in opposite directions, until the new nest is definitely chosen. In a case like this the first new nest is soon abandoned, as we saw in Chapter II*b* in connection with the fission of a colony of *F. pratensis*, when separate divisions emigrated from *A* to *B*, *C*, *D*, and *E*. Migrations sometimes take place in different directions, towards two new nests at the same time; as a rule, but not always, one of these is afterwards abandoned in a new move, either direct or by way of the old nest.

Huber was first again in observing ant-migrations, basing his study on *F. rufa* and *pratensis*. These ants carry one another as shown in fig. 83. The ant that is being transported curls up her limbs under the body of the recruiter, which has first invited her to do so by grasping her with its mandibles, but she feels and sees her way nevertheless, for she always finds it again by herself. The genera *Formica*, *Camponotus* and *Cataglyphis* (as I saw in Tunis) carry each other in the same fashion. Some ants carry their companions the other way about, that is, upside down on their own backs, holding their mandibles, as it were, back to back; this happens, for instance, with *Tetramorium* and *Leptothorax*. Yet others, such as *Tapinoma*, grasp their companions by the body, as shown in fig. 84. The one that is carried always folds up her legs and, to a certain extent, her antennæ. According to Wheeler, *Leptogenys* transports its ♂ between its long legs, taking hold of them by the neck.

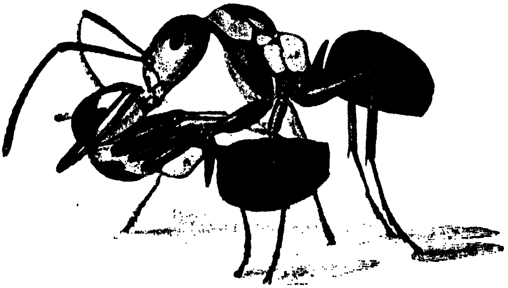

Fig. 83

Ants with good topochemical smell have no need of mutual transportation. They follow each other by the sense

Fig. 84

of smell. This is the case, for instance, with *Lasius*, the *Dorylinæ*, and various *Myrmicinæ*, while *Formica* and *Camponotus* proceed by transportation. According to Santschi, fig. 85, which is explained in Chapter I, Part II, proves the visual orientation of certain ants. The recruiting ant and those which afterwards imitate her are as busy as they are insistent in urging their companions to follow them. They do this by means of their antennal language or headblows, or even by abruptly seizing one another. The ant thus assailed sometimes offers a certain amount of resistance. *Lasius* contents herself with antennal speech, *Tapinoma* touches with her abdomen, as she walks, the track to be followed, and impregnates it with the odour of her anal glands; most of the others then follow her.

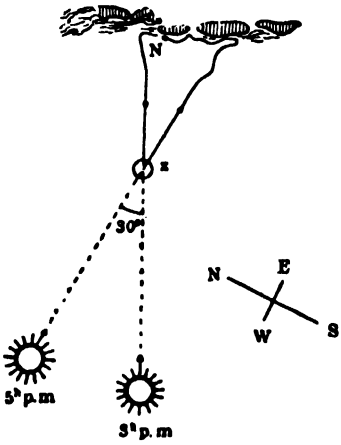

Fig. 85

Vosseler gives the following account of the migrations of the African *Dorylinæ* (*Anomma*). When the carnivorous *Anomma* (Siafu) have exhausted their hunting-area, they gather together and decide to emigrate with their entire equipment. They make preparations by going and pillaging the nest of some species of *Myrmicinæ*, for example, situated 400 metres away, on the confines of the area they have already ravaged, and driving away its inhabitants, not without some fighting and casualties. For this purpose they rapidly construct a covered path, level with the ground where it is bare, but not where the grass protects them from the sun. A short rest precedes the departure. Soldiers mount guard over the passage all the way along. At 9 o'clock in the morning, a dusky troop leaves the nest by way of the covered gallery. Every ☿ carries a larva or a naked nymph. The exodus lasts for about twenty-four hours, day and night. The queen mother, the ♂, the guests, the whole formicary marches or is carried out. At 9 p.m. the masses are as thick as in the morning; about 9 o'clock next morning the last workers leave the old nest, carrying nothing more. To protect the migration, cohorts of large ☿ (or ♃) guard the weak or open parts of the gallery, or the places in the thick grass where there is no covered gallery. Directly the last emigrants have passed, the troop of guardians begins to follow them.

The old nest which he saw had been taken from a species of *Myrmicinæ* whose brood had also been stolen and eaten by the *Anomma*; they had afterwards broadened and modified the nest in question for their purpose and replaced the devoured brood by their own. They had sojourned in this nest for only eleven days, to extend their insect-hunting over a surface of about 10,000 square metres, in a country covered with low-growing vegetation. Vosseler estimates the duration of the sojourn of the *Anomma*, in the intervals of their migrations, at 8-15 days. Between five and seven laden ants passed by per second, and hence about 720 (including nymphs) per minute, which makes a total of 1,036,800 in the twenty-four hours. But to this must be added the whole troop of guardians and the invaders which had rifled the nest before the removal. Vosseler estimates the population of this comparatively weak colony at about two million inhabitants.

Müller, too, has observed at Itajahy in Brazil the migrations of *Eciton Burchelli*, which he described in 1886, and which take place chiefly at night. These *Eciton* ants have no nests, but prefer to dwell in hollow tree-trunks. Sometimes they merely form an ant-bundle in the open air, as Belt had previously remarked. The ☿ transport the larvæ and the nymphs in their woven cocoons. The ♂ also follow the trek which may extend to a distance of 200 paces from the old haunt of the brigand community. In other respects everything happens as with the *Anomma*, including the rest period which precedes the migration.

As early as 1865, I had taken advantage of the migration of a *Formica pratensis* colony to calculate its numbers, which were, very roughly, about 114,000, and I had supposed that according to circumstances the population of a *pratensis* formicary could vary from 5,000 to 500,000 inhabitants for a single nest. Other authors, especially Young, have made lower estimates, and think that I was exaggerating. The future must decide who is right. It is evident that the ants which carry their companions in their migrations are obliged to do so because they have no way of making them follow. It is mainly *Formica* and *Camponotus* which are in this predicament. I here refer my readers to what I said in Part II, Chapters I and II, with regard to the sensations of ants, etc.

10 GAMES. We already find mention of the games played by ants in Gould. Speaking of a colony of *F. pratensis*, Huber writes:

"None of them was working; this multitude of insects gave the impression of a liquid in effervescence, upon which the eye could scarcely at first fix its attention. But when I set myself to follow single ants, I saw them approach each other, waving their antennæ about at an astonishing rate; their fore-legs were making light, fawning movements against the sides of the heads of other ants. After these first gestures, which looked like caresses, they were seen to rear up on their hind legs in pairs and wrestle together, seize each other by a mandible, a leg or an antenna, and fall quickly back, only to come again to the attack; they clung to each other's armour or abdomen, embraced each other, rolled over on their backs and rose again, and took their revenge upon one another without appearing to do any harm; they did not eject poison, as in their battles, and did not engage their adversaries with that obstinacy which we have noticed in their serious quarrels; they soon released the ants they had seized, and tried to catch others. I saw some which were so engrossed in these exercises that they pursued several workers in succession and wrestled with them for a few moments. The combat only came to an end when the one with less vitality, after overturning her antagonist, succeeded in escaping and hiding in some gallery. I returned to this nest several times and always saw the same thing. There were groups of ants fighting everywhere, and I never saw a single one come out of the fray wounded or mutilated.

The other nests rarely entertained me with such behaviour, half warlike and half social; for though the customs of ants of the same species are essentially similar, very distinct shades may be noticed between the habits of one tribe and those of another."

I had always been sceptical about this, but later on I myself observed a similar performance. Workers seized each other by the legs or the mandibles, rolled about on the earth, then released each other and dragged various ants into the holes of their dome, whence they came out again shortly after, etc. In all this there was no sign of bitterness, and no poison was ejected: it is evident that the performance was of a purely friendly nature. If I blew ever so lightly upon them I put an end to their games. I admit that to anyone who has not seen it, all this may appear to be imaginary, for we must remember that sex-attraction cannot be the cause of it. To-day, it might, perhaps, be described by Freud as 'sublimated love.'

In 1918, Stumper made similar observations with the little ant *Formicoxenus nitidulus*, a guest of *F. pratensis* and *rufa*. He tells us that he saw some workers of the same colony struggling with one another, taking hold of each other by the legs or mandibles, amusing themselves by rolling on top of one another, feigning flight, and beginning over and over again this child's play of sham fighting. In 1919, Dr. Stäger of Berne (*Erlebnisse mit Insekten*) confirmed Stumper's statements by his observations on the games of *Formicoxenus* in formicaries high up in the Alps.

It is a well-established fact, therefore, that on fine, calm days when they are feeling no hunger or any other cause for anxiety, certain ants entertain themselves with sham fights, without doing each other any harm; but these games come to to an end directly they are scared. This is one of their most amusing habits.

11 LASIUS (*Acanthomyops*) LATIPES AND MELISSOTARSUS BECCARII. Wheeler has carefully observed the nuptial flight

and the large formicaries of this curious ant from Illinois and Connecticut in the United States. It has two kinds of ♀, *A* and *B*, both of which are winged and share the nuptial flight in the air, but only a single form in the ♂ and the ☿. The *B* ♀ is represented in fig. 86, with her tibiæ and thighs enormously broadened and flattened, and her antennary funicles likewise greatly thickened. The *A* ♀ is smaller, narrower and lighter in colour, and her thighs and tibiæ are almost common-place, though a little thicker than those of her neighbour, *L. claviger*, which inhabits the same district but has a slighter funicle. The reason for the presence of these dimorphous ♀, which are always distinct from each other, without any transition, remains an enigma. Both certainly belong to one species and neither to a parasitic species, for the males and ☿ are all identical. The *A*-♀ mingles with the *B* in the nuptial flights, and both are found in Connecticut as well as Illinois. There can be no question of this being pathological, nor, in my opinion, can it be the result of hybridization. Wheeler, nevertheless, shows the theoretical possibility of hybridization with *L. claviger*. The cause of the flattening and broadening of the thighs and tibiæ in the *B* ♀ has still to be discovered. Possibly it is of use for digging in the earth.

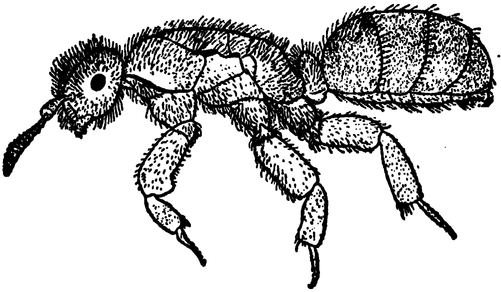

Fig. 86

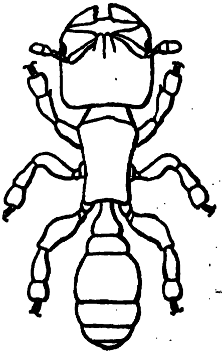

Fig. 87

Melissotarsus, whose ♃ is shown in fig. 87, is another curiosity—this time from Africa. The first joint of the tarsus, in particular, is absurdly thick, both in the worker and the soldier—for what purpose we cannot tell, as the creature's habits are unknown.

Chapter IV

THE ART OF BUILDING

In Chapter VI of Part II, I described the extremely diverse forms of nests built by ants, and their constructions outside the nest. To avoid repeating myself, I must refer to this chapter; here I wish to explain how our little friends set to work to build these collective nests.

In order to do this we must first examine their tools, which were also described in our first Part, in connection with anatomy, and reference may be made to this.

1 Tools. The most important of the ants' tools are their mandibles. To realize how far the forms of these tools differ according to species and often according to the polymorphism of the same species, it is enough to glance at the different ant-heads depicted in figs. 3 and 6 (Part I). Short, well-curved mandibles, furnished with a few strong teeth and moved by powerful muscles, are used for gnawing wood, grinding seeds or cutting up insects. Mandibles which are less massive and more finely dentated are used for digging and carrying earth and constructing masonry with it. When the ♃ has long, toothless hooks by which to grapple with enemies and bite them, or when large and medium-sized ☿ have sharp, triangular mandibles with which to cut leaves, we find small ☿ with dentated mandibles for domestic and masonry work, etc. There are cases, however, which we do not as yet understand very well. All

the ☿ of the true *Leptogenys* have long, narrow mandibles, wide at the base and toothless. Wheeler says that *Leptogenys* uses them for piercing the heads of termites and killing them for food. That is all very well, but it does not explain how these ants build their nests in decayed tree-trunks, or why other ants which eat termites have toothed mandibles. If we have patience, the future will divulge the truth to us.

By an alternating movement of their toothed mandibles, ants likewise saw through plant-twigs, and when closed the same instruments are used to press against damp earth.

Next in importance are the legs, especially the hind ones, which are used for clearing the ground and probing in dry earth, sand and débris. The small claws of the tarsi are utilized to cling on vertical walls in climbing. The legs also serve for dragging heavy weights—when walking backwards—while the antennæ search for odours and the palpi touch objects. The head, abdomen and maxillary palpi are sometimes also used as tools.

We have already mentioned the psammophores depicted in fig. 11 (Part I), which are used by desert ants, together with their maxillary palpi, for transporting loose grains of the finest sand. Such are the principal tools used by ants, not to mention the saliva of their glands, which serves to glue together the small scraps of material used in carton-making. As for the weaving ants which use their larvæ as tools, we will reserve them for Part V. It is plain that there is no lack of variety.

2 Miners. There are two kinds of pure miners, which confine themselves to mining earth with their mandibles and legs. One kind, with the intention of hiding, as far as possible, the entrance to their nests, carry earth as far as they are able; nothing can be seen but a little hole on a level with the ground, and sometimes even this is blocked. The

other kind use the earth or sand which they have extracted during their subterranean labours to construct, all round the opening, the craters which we have described and pictured. The subterranean passages and their chambers are the sole product of this elementary art, whose tools are mandibles, legs and psammophores.

3 MASONS. I use this term as Huber uses it, to denote the ants which erect above their underground dwelling, immediately after rain, a dome of earth constructed, or made of masonry, by themselves. The art varies with the species, and Huber has given an admirable description of it in the case of *Lasius niger* and *Formica fusca.* In the same illustration, fig. 102 (Part IV), the network of chambers of *Formica fusca*, with their rough grained work marked *For.* may be compared with those of *Solenopsis fugax* with its fine grained work *S.* The ☿ of *Lasius niger* (see their nest in fig. 49, Part II) build a new storey to their dome immediately after rain. They open up its surface in several places with their mandibles, and bring up to it from every side small pellets of damp earth scraped from the bottom of the underground passage with the tips of their mandibles and carried between their teeth. Each ☿ then lays a bit in its place in the new storey that is being built, divides it up and thrusts it in with her teeth, filling all the inequalities of the walls or chambers in process of construction. She probes every particle of earth with her antennæ, and then presses it lightly between her front legs to strengthen it. Within a few hours everything is complete—walls, one millimetre or several millimetres thick, pillars, galleries and the whole structure. To the onlooker the work seems to have been carried out by magic; he cannot understand how every ☿ divines the intention of the others and avoids disturbing their work. None the less, one of them occasionally corrects

some error committed by another. If the preceding storey is convex, the new one is made like it, and despite the irregularity of the details, we perceive an instinctive common plan growing clearer and clearer.

As soon as the pillars and walls have attained an average height of 1 centimetre, the next business in hand is the construction of the ceilings. For this purpose relief is given to the surface, new pellets of earth are added, and the ☿ build an arched vault for every roughly-planned chamber, thickening the curve between the wall and the ceiling. Huber has given an admirable account of the curious spectacle presented by the various ☿ working at different sides of the ceiling and contriving to meet in the horizontal centre of the vault without committing any serious error. If you look at the figure I have mentioned, dear reader, you will understand—but the best way of judging is to observe for yourself. You see that *L. niger* utilizes the blades of grass and the leaves merely as starting-points, and does not saw or bend them. Near the centre of the nest, in particular, we observe large crosspieces, from 3 to 6 centimetres broad, as described by Huber, the common vault being supported by buttressed pillars, constructed like the walls and chambers.

Huber tells us that in spring or early summer *L. niger* may be seen building as many as twenty of these new nest storeys. He frequently arrived on the scene in the morning to find that a new storey had been constructed during the night. The ants in question require no more than seven or eight hours in which to add a storey to their dome by communal workmanship. But in the autumn, and more especially in the winter, all this labour is gradually effaced, so that it has to be begun all over again, to a great extent at any rate, the following spring. The convex storeys in an intact *L. niger* nest are the most regular, the most elegant and the least massive. The domes of *L. flavus*, which otherwise builds in the same way, are more irregular and have less clearly-defined storeys, and the same features are even more exaggerated in the work of *Serviformica*. As Huber says, we must not forget that the damp earth from which the ants form their masonry is taken from their underground dwellings, whose cavities increase in size accordingly.

In this fashion, therefore, our masons carry on a double work, first at the bottom of the nest and secondly above in the dome, thus providing ordinary accommodation on the one hand for their brood and their major sexual forms, and, on the other, accommodation for this same brood when extreme heat by day or extreme cold by night makes it convenient to seek shelter underground.

We come now to *Serviformica fusca*, which was so well observed by Huber. From the subterranean nest she brings in her mandibles a thick layer of damp earth, and in this layer the workers hollow out or carve in relief the plan of a new storey, constructing the walls with the earth they have taken from the floor. Presently only the vault of the ceiling remains to be built. The ☿ of *F. fusca* is larger and more markedly individual than that of *L. niger*, and her labours may be studied more easily.

For example, one ☿ brings some damp earth to a certain place where she digs a groove all by herself and forms a gallery 6 centimetres long, leading to a chamber. She works with such precision that Huber could foretell which fragment she would remove. The same ☿ next constructs a second gallery leading to another chamber-opening situated quite near and separated from the first by a little wall. But I will leave the rest of the story to Huber:

"A wall was raised on this spot; it seemed to be placed with a view to sustaining a still unfinished vault thrown from the opposite end of a large chamber; but the worker which began the vault had not made it high enough for the wall on which it had to rest; if it had been continued in the same plane, it would inevitably have encountered this wall half-way up, and that was just what had to be avoided. This critical point was deservedly occupying my attention when an ant arrived on the scene and inspected the works, after which she appeared to be struck by the same difficulty, for she began, as I watched her, to destroy the unfinished vault, then raised the wall on which it rested and made a new vault with the débris of the old.

It is chiefly when ants are beginning some enterprise that we may expect to see an idea awaken in their minds and express itself in action. Thus when one of them discovers on the nest two blades of grass which cross each other and may favour the formation of a compartment, or some small twigs which suggest the angles and sides of such a compartment, you see her examine the parts of this whole and then place particles of earth in the empty spaces and along the stalks, taking her materials from any place convenient; sometimes she even takes no notice of the work which others have begun, so entirely is she dominated by the idea which she has conceived, and which she follows up without allowing anything to distract her. She goes to and fro at her task until her plan has become clear to other ants.

In another part of the same nest, several bits of straw seemed to have been placed on purpose to form the timber-work of the roof of a large chamber. A worker took advantage of this arrangement. The fragments, lying horizontally, half an inch from the ground, crossed each other to form a long parallelogram, and the industrious insect first placed earth in all the angles of this timbering, and along the little twigs of which it was composed. The same worker laid down several rows of these materials, one against the other, so that the roof of this chamber seemed to be very distinct, but then appeared to notice the possibility of profiting by another plant to rest a vertical wall against it, and accordingly laid the foundation of this new wall as well. Other ants having arrived by that time, they finished together the work which the first had begun."

Formica fusca r. *glebaria*, after making an inspection, often utilizes the leaves of Gramineæ, placing earth upon them to force them down, and the stalks, sawing half-way through them with her mandibles—all to the same end, namely, the strengthening of the vaults of her chambers at the height desired. Think not, dear reader, I beg you, that these are fairy tales, or that ants reason as men do. Remember that this, for the most part, is the result of instinct, the hereditary mneme proper to each species. But the memory acquired by each worker is duly superimposed upon it and modifies, to some extent, its individual actions, and this, combined with the irregularity of the ants' constructions, makes their instincts appear much more rational than they really are. Here I refer you to the second chapter of Part II.

The proof of this is, briefly, that every kindred race or species of *Serviformica*, *subsericea*, *fusca*, *glebaria*, *rufibarbis*, *gagates*, *cinerea*, *picea*, etc., has a specific architectural instinct which strictly limits individual modifications. For instance, the true *fusca*, properly so called, prefers the underside of stones; *rufibarbis* favours more mining and less masonry, and makes her nest more open; *cinerea* is similar, and furthermore, she works chiefly in sandy regions, where she forms polycalic colonies; *picea*, like *F. rufa*, whose building art has been described by Huber, even makes her nest out of mixed materials.

If we turn now to the purely temporary domes of *Tapinoma erraticum*, shown in fig. 48, Part II, we find evidence of a simpler system. The ☿ often use nothing but a tuft of grass on which to build up their somewhat rough dome, making the stems and leaves a support for the whole. In other respects they work in the same way as those previously described, and when necessary they also frequently build a few intermediate walls or even a small dome of pure masonry, which is invariably weak and carelessly made.

Tetramorium cæspitum, *Myrmica rubra* and its kindred, *Monorium Salomonis*, *Aphænogaster*, *Pogonomyrmex* and many other ants, construct domes of earth-masonry in a fashion more or less analogous to that of our *Serviformica*, but less artistically.

Certain ants of Colombia and Asia, *Pheidole vallifica*, *præusta* and *Sykesi*, surround the opening of their nest, which is mined only, with a rampart. This rampart, spread out at the top like a flower, and described in Chapter IV *A*, Part II, may be single or multiple, but it is always concentrated about the exit-door and constructed of simple masonry, like that of *Conomyrma Wolfhügeli* and the upraised, solid exit-tubes seen in the work of the American *Möllerius* and certain *Trachymyrmex*. How and why these ants carry out work of this sort, whether, for instance, they mingle the saliva of their mandibular glands with the mixture, to make it more solid, is so far unknown. These calices and tubes may be seen in figs. 46 and 47, Part II.

Certain *Pogonomyrmex* of Texas and Mexico, races of *P. barbatus*, replace their crater by a round surface 1 or 2 metres in diameter, which they clear of all vegetation by sawing with their mandibles through the bases of all the stems of grasses which originally overgrew it. Figure 88 represents this phenomenon under natural conditions on the steppes of Arizona. Wheeler states that the aim of this clearing process is to procure a maximum of dryness in the ant-granaries which are situated immediately under the cleared surface. These same ants often stop up the entrance to their nests with a heap of little stones.

Fig. 88

4 Constructions in Sand. We are indebted to Santschi for demonstrating the purpose of the *psammophores* or rather *macrochætes* (long hairs) described and depicted in figure 11, *A* and *B* (Part I). Santschi found that pellets of damp sand, such as those shown in figure 52 (Part II) were carried by *Messor* between its mandibles, like those which are made of earth, and he gives the following account (Santschi,

Revue zool. suisse, 1909, p. 451-452): "When the sand is dry and shifting, and has not to be transported far, *Messor arenarius* digs it by scratching it up rapidly with her front legs and throwing it behind her as a terrier would, but always moving backward as she does so. The largest individuals, however, prefer to use their heads, whose lower part is more or less concave, like a spade. To do this, the ant lowers the front part of her head into the sand and walks backwards, drawing behind her mandibles and head a small heap of sand, which she takes with her. If the little heap of sand has to be seized and transported, the ant is seen to check her retrograde course, pile it up with her front legs a little to the side and right in front of her mandibles, and then lift it like a pellet (much smaller than the one made out of damp sand), which remains hung beneath her head and between her mandibles. There is then nothing to prevent the animal from carrying her burden a long distance. When she reaches her destination, she opens her mandibles and the sand rolls out on to the ground. It is difficult to understand how the mandibles alone could carry the dry, shifting sand if they were not assisted by rows of stiff hairs surrounding the mouth, where they form a kind of cage or basket." Santschi adds:

"*Messor barbarus* has a comical way of carrying sand. Bending her head and resting her forehead on the ground, she props herself up on her four back legs, curves her abdomen underneath her thorax in such a way that its extremity pushes and heaps up the sand in the macrochætes under the head, while the front legs compress it laterally. When she has a firm hold on her burden, the insect stands up again and the sand is retained under her head. Sometimes it lodges there so persistently that the ant is obliged to use her legs to rid herself of it."

To the above-mentioned figure 11 *A* my readers must add in imagination a ball of loose sand under the head and between the mandibles, the posterior edge of the head and the slightly parted psammophores of *Messor Pergandei*, which is depicted there. They will then see her in the mind's eye, carrying her sand.

In *Cataglyphis bicolor* and *albicans*, Santschi has observed that the sand is held by very long maxillary palpi, much farther to the front than in *Messor*, aided by the anterior and lateral psammophores; for this purpose the ant stretches them in front of her. This is even more applicable to *Machæromyrma bombycina*, and to *Dorymyrmex* and *Conomyrma* of the desert, which have enormous, hairy maxillary palpi. But this is not all.

The head itself is often deeply compressed on the under-side, as in *Messor caviceps*, *Dorymyrmex ensifer* (Plate IV*C*, Part II), etc. This depression is now regarded as providing more room for the balls of dry sand. Hence all these convergences in form among desert-ants—psammophores, long and hairy palpi, heads with flattened under-surface, are all quite naturally explained by Santschi's observations. In *Camponotus mystaceus*, some of the macrochætes are situated between the frontal area and the epistoma. Santschi sums up the matter as follows (Santschi, *Revue zool. suisse*, 1909, p. 458):

"1st. Most large arenicolous ants are provided with a psammophore apparatus, intended to hold and transport sand.

2nd. This psammophore is composed of: (*a*) mandibles whose deficiencies are compensated for (*b*) by several rows of long hairs, the macrochætes (those of the epistoma, mandibles, under-side of the head, sides and back of the mouth, and finally the palpi), to which are sometimes added (*c*) the maxillary palpi and (*d*) the flattening of the lower surface of the head.

3rd. The situation of the psammophore varies with its composition, according to the species. In most of the *Myrmicinæ* it is thrust to the back, in certain *Cataglyphis* farther to the front, between the mandibles, and in *Camponotus mystaceus* and its varieties, rather in front of the mandibles.

4th. Ants pack the sand into their psammophores by means of their mandibles, head, front legs and sometimes their abdomens.

5th. The development of the psammophore is in direct ratio to the abundance of sand and the dryness of the environment."

By 'psammophore' Santschi means the *whole* apparatus used for carrying mobile sand, and by 'macrochætes,' the long hairs more especially intended for this purpose.

5 WORK IN COMPOUND NESTS. Here the ants simply use their mandibles to transport and amass under their dome the mobile materials of which it is composed; fir and pine needles, fragments torn from grasses—sometimes sawn through by the ants themselves—small shells, scraps of leaves, etc. These materials are gradually interwoven so as to close the interior labyrinth of the nest by successive displacements. The masonry and the mined part of the nest are made in the same way as those of *F. fusca* but *F. rufa*, *exsecta*, etc. and their races combine the above materials with their earth-masonry at the base of their nest. As they are larger and live out in the daylight on their dome, anyone may observe their work at his leisure. It is highly diverting to see them close their doors in the evening and open them in the morning. Here I will let Huber continue the story, in connection with *Formica pratensis:*

"I saw clearly, therefore, that they were toiling to close their passages; for this purpose they first brought small twigs near to the galleries whose entrances they wished to make smaller; these they placed above the opening, sometimes even burying them in the mass of thatch. They next went in search of more twigs which they arranged above the first, in the opposite direction, apparently choosing less substantial ones as the work advanced; finally they used pieces of dried leaves or other materials of a broader shape, to cover up the whole.

I was impatient to find out what happened on these nests in the morning, and accordingly one day I paid them a very early visit. I found them still in the state in which I had seen them the day before. A few ants were gnawing at the outside of the nest. From time to time, however, one of them would come out from under the edges of the little roofs built at the entrance to the galleries, and soon I perceived some of them trying to remove the barricades. They succeeded with ease. This work occupied them for several hours, and presently I saw the passages free of all obstacles, and the materials which had obstructed them spread about all over the nest."

Huber is right in saying that *F. pratensis* and *rufa* leave their doors closed when it rains, and that the architecture protects then at the same time from damp and cold. On the other hand, he is wrong in believing that they *always* close their doors in the evening. During the dog-days, they leave them open and work at night.

In August, 1914, I myself saw a *Serviformica picea* colony whose nest I had destroyed, promptly rebuild it with fragments of Cyperaceæ (*Schœnus ferrugineus*), and in absolutely the same manner as *F. pratensis*, but in miniature. They interlaced various *Schœnus* filaments with which to build a labyrinth of chambers, opening and closing their doors, etc. This species, therefore, produces the same kind of architecture as the *Formica rufa* and *exsecta* group; but in the damp earth of the formicaries I could not clearly distinguish the masonry base in building-work carried out in such a frail material.

So far as I know, the manner in which tropical ants build their compound nests has not been studied.

6 WORK IN WOOD AND BARK. It is very difficult, not to say impossible, to observe exactly how *Camponotus herculeanus* and other wood-gnawing ants set to work to sculpture the interior of their tree. But the power of the large ☿'s mandibles, which cut through the head of an enemy in one bite, shows plainly enough that she is the sculptor. Moreover, the structure of the nest proves that she does most of her carving in the softest parts of the wood. It is the same with little *Leptothorax*, which carves the under side of the bark; we may see the result, but not the labourer at work.

7 CARTON-MAKING. No myrmecologist has yet succeeded in observing how the carton-building ants go to work to make their carton, which is so frequent, however, in the tropics. Huber was mistaken in supposing that our *D. fuliginosus* gnawed wood, but neither he nor I, despite our patient experiments, was ever able to see it make its nest. Everyone has agreed, as though to a dogma, that it is the glutinous secretion of the ant that is generally employed to make carton out of rotten wood, various kinds of refuse, and sometimes earth, sand or small stones, as in the case of wasps and other Hymenoptera. With regard to *Azteca*, *Cremastogaster* and other tropical ants, whose carton nests hang from the trees, and have to be built in daylight, I am sure that a little patience and observation on the spot would suffice to reveal how these artisans go about their work.

For that matter, the details of the vegetable fibres composing many carton nests—those of *Camponotus Göldii* and *Cremastogaster Ranavalonæ*, etc., which can be seen in fig. 57, and plate III of Part II—are so distinct that no doubt as to their nature can remain. The only doubtful points are the origin of the substance which binds them and the manner in which the ants proceed with the construction. Here, once again, we must await further evidence.

Apart from the work of *Dendrolasius* and *Liometopum microcephalum*, I found at Nîmes and Dielefit (Drôme), about the year 1904, some fairly strong ligneous carton nests, built under stones or among roots by *Cremastogaster scutellaris* of Europe. Krausse and Wasmann have also pointed them out. Brun and Donisthorpe likewise speak of carton nests belonging to our *Lasius umbratus* and *emarginatus*, but the carton in question is of very poor quality, and can be destroyed by the least pressure, like that of *Lasius brunneus* and *bicornis*. This last case forms a transition to simple masonry of earth and sawdust. It is evident that no one can check the operations to see whether the building ants add or do not add a little of their mandibular saliva. Here, I presume, we have the transition between masonry and carton-making.

8 Weaving Ants. We shall make special mention of the weaving ant in Part V. On this occasion, the larvæ are used as tools, that is, as weaving-shuttles. I only refer to the matter here for the sake of completeness, and to mention the additional fact that all possible combinations between the art of weaving and that of carton-making are to be found among ants.

9 Construction of Open and Covered Roads. Grasslands are virgin forests for the ants, and would sometimes be inaccessible to them but for the fact that they can climb up

every stem or grass blade with their six legs, by means of the claws on their tarsi. The small species swarm about without any trouble on the earth, among the grasses, but the large ones, especially when laden with building material or prey, find incredible difficulty in advancing. The objects they are carrying are constantly being brought to a standstill, jerked away or caught between two stems; this means going backwards and overcoming the obstacle by extraordinary muscular efforts. We have only to observe attentively the manœuvres of *Formica pratensis* in our meadows to admire the perseverance with which she transports her burdens. But she also seems to us more clumsy in this respect than other ants. This is evidently the reason why she takes so much trouble in constructing the open roads we mentioned in Chapter VI *B*, p. 174, 4 centimetres broad by 1 to 1½ deep, clearing away the earth and sawing through the stems of the Gramineæ and other plants with her mandibles. Wherever the stems are too large, the road twists round them. In short, this road meanders somewhat from point to point, but it follows one definite general direction, towards a tree or some other object to be exploited. According to its size, every *pratensis* colony has one, two, three, four, five, six, seven or even more paths, radiating from the nest to a distance of 10, 30, 50 or 60 metres.

To appreciate the work which the upkeep of these roads imposes upon the ants, you must bear in mind, dear reader, the vigour and rapidity with which grass grows, the ravages of the sickle, the second hay-harvest in July or August, etc. To keep their roads in order, the ants must be continually sawing, clearing, transporting and digging. I may remind you of Sernander's calculations and my own, in Chapter III of Part II, as to the number of seeds and insects (four per minute) transported by *F. pratensis* on a single one of her paths. The authors who thought that these paths were formed merely by the tread of the ants were certainly very innocent.

F. pratensis drains the whole field in the intervals between her open paths, which, like our roads, are only large arteries for circulation, designed to facilitate the travelling of the laden ☿. The open roads of *Formica rufa* are wider, but less distinct; those of *Dendrolasius* are narrow, but often quite indistinct.

Fig. 89 represents in natural size the building of a covered path by *Lasius niger*, after rain. I took M. Heinrich to the spot, and he at once drew from nature the ant-masons which were building up their covered path with pellets of damp earth, passing under a small branch. You may see in the figure how the ☿ carry their little bundles of earth and two of them, coming out through the openings, lay down their pellets close together, to reinforce the masonry or make the hole narrower. Best of all, this figure will show my

Fig. 89

readers how this mason-ant constructs covered paths of this sort across cleared spaces, enabling large numbers of ☿ to go to and fro under shelter and find food or milk their aphids. We saw above how *Anomma* produces similar constructions in Africa when she is moving quarters, as *Eciton prædator* does when going in search of prey.

In Chapter III of Part II, I also mentioned the covered paths built out of various materials, for the same purpose, by *Formica integra* of the United States, as well as the tubes built in the Gramineæ by *Polyrhachis Zopyrus*, rising above her nest in Java.

We have already seen how blind ants, or those with poor sight, go hunting and foraging underground and mining subterranean passages everywhere; we shall mention this matter again in our next chapter while dealing with aphids.

10 Pavilions and Succursals. The art of constructing pavilions and succursal nests, either with earth or carton or in some other fashion, is the same on a small scale as that of building the corresponding nests. I will content myself here with referring my readers to figs. 92 and 93, which we discussed in connection with the aphids, as well as fig. 57 (Part II), which represents two little carton succursals of a *Camponotus Göldii* nest.

11 Open Air. Some ants dispense with architecture and nest in the open air. Among these are *Eciton*, which Belt saw in Nicaragua, rolled up in a great living ball around the brood and using the tropical bushes as nests, or rather as temporary hunting-camps; the species *Acromyrmex octospinosus*, which make fungus-gardens in the open air in the Brazilian brushwood, and certain *Cremastogaster scutellaris*, which I myself saw in Ticino warming its brood, which had no cover whatever, between the large stones of an

uncemented wall. I presume, nevertheless, that the *Cremastogaster* of Ticino had also carton nests underground. For the rest, *Lasius emarginatus*, which lives in cracks between the stones of our houses, and all the ants which build nests without carton, simply in natural vegetable cavities, also dispense with architecture.

12 IRRIGATION. Miss Fielde has observed a most curious and interesting fact. She had assembled between 100 and 200 *Aphænogaster picea* ☿ and left them on a heap of dry earth upon an artificial nest built on the Lubbock system. The following night, she tells us, these ants went to drink water from the canal which surrounded the nest, thus moistening a good deal of piled up earth, and there they constructed a very tidy nest. When Miss Fielde arrived the following morning, the ants were busily employed in laying their larvæ here, in chambers of their own building. Miss Fielde thinks that they had lapped up this water in their buccal sacs.

I do not think this was so, as the buccal sac is too small and too full of solid matter. I believe that if the observation is correct, we are confronted here with a fact of capital importance, namely, the use of the crop as an instrument of irrigation in a case of urgent necesssity.

In June, 1921, in the presence and with the assistance of Prof. Leininger of Karlsruhe, I made the following control experiment at Yvorne. We placed upside down in a large tub full of water a china soup tureen with a hollow foot. The hollow was large enough to house the ants, with their brood and some very dry earth, broken up into minute grains. To enable the ants to go and drink without falling into the water, the foot of the tureen was surrounded at the top with wool, but the narrow portion between the foot and the bowl (intended for soup) was left free. Lower down, however, on the convex part of the tureen, I put a strip of rather fine cloth which dipped into the water. This band, and this only, immediately became wet.

On this we placed some *Lasius niger* and their larvæ and cocoons in the hollow foot of the tureen, with some fragments of dry earth. They went to drink, certainly, but instead of moistening the earth and building, they only managed to lower some of their brood on to the band of damp cloth, leaving most of it on dry ground. The experiment was continued for two days, with an entirely negative result. The *Lasius niger* evidently regurgitated honey-dew to the larvæ which remained dry but did not moisten a single bit of earth or make any attempt at building. All the material remained dry and friable.

We afterwards repeated the same experiment with some large *Myrmica* (*Neomyrma*) *rubida*, still more carefully, and again the test lasted for two whole days. The result was likewise absolutely negative. Are we to deduce from this that Miss Fielde was mistaken, or that our experiment was unsuccessful, or perhaps that American ants are more intelligent than those of Europe, as my colleague Leininger suggested? The answer will doubtless be forthcoming in due course.

Chapter V

ANT-CATTLE AND THEIR FOOD

Many ants rear cattle, but only to milk them, not to bleed or slaughter them afterwards, as we do. This is what Wasmann and Escherich call *Trophobiosis*, which means 'nourishing life.' I consider this term unfortunate, since it is a pleonasm: all life depends upon food. Moreover, it does not indicate the symbiosis (life with) between ants and their cattle. We ought rather to say 'Synctenobiosis' (life with cattle)—but enough of Greek words.

In Part II we discussed myrmecophilous guests, and we saw that they are shameless and hypocritical exploiters. For the most part they do a great deal of harm to the community which entertains them, and often feeds them and their larvæ. We have also mentioned plants which provide the ants with nests. In Part V we shall speak of those which feed them with their seeds, or indirectly with their leaves. We have also discussed mutual help or syndiacony, between ants and plants. As we shall see, it is under this last heading that we may best place the relations between ants and their cattle. These cattle really derive almost as much advantage from the ants as their exploiters do from them. They are not wretched slaves, like ours; real mutual service is rendered, although the cattle are somewhat dependent upon their ants. The only beings which are robbed and exploited in this transaction are the plants, and indirectly man, who feeds on them.

Ant-cattle consist chiefly of aphids, and secondly of their near relations the coccids or gall-insects. Then come various Hemiptera, *Centrotus*, *Tettigometra*, *Cercopis* and Membracidæ, and in Australia, according to Froggatt, the Psyllidæ. Finally, there are certain caterpillars of the Lycænid butterflies which ants use as cattle in a similar fashion. Schouteden has found no less than seventeen different species of aphids serving as milch-cows to *Lasius niger* alone; Wasmann has counted four to *Lasius flavus*.

I APHIDS AND COCCIDS. As a rule it is not any kind of special secretion, but the actual excrements of their cattle, which ants milk, or rather swallow, simply by gulping them down into their crops. It seems strange that excrement should be so nourishing, but it is a fact that the excrement of aphids and coccids, and probably also that of other ant-cattle, is very sweet and is eliminated in the form of honey-dew. It is exuded in drops, transparent, sweet and glutinous, which must be due to the imperfect digestion of the juices which these insects extract from plants.

If you know anything of the country, friend reader, though it be only your garden, you have certainly seen aphids—plant-lice or rose blight—which, together with the coccids (scale-insects, mealy bugs) are the despair of floriculturists and market-gardeners, swarming on their flowers and even more on their vegetables and fruit-trees, which they ruin—peach trees, apple trees, plum trees, beans, etc. Ants help them to swarm still thicker by protecting them from their enemies and rearing them. Huber was the first to discover the principal facts about this matter, as about most others.

He noticed that when there are no ants, the aphids get rid of their excrement from time to time by kicking with their legs. The leaves in their vicinity are then bestrewn with sweet, sticky honey-dew, which various insects lick up. But Huber observed that when the ants are keeping these aphids, they tap them with their antennæ, one after the other, in a friendly manner. Then, almost invariably, the aphid slowly emits a drop of liquid from its abdomen, without a kick. The ant immediately swallows this drop through its mouth, then passes on to another aphid, and so on, till its crop is full. Thus the suction of plant-juices by the aphids is powerfully stimulated, and so likewise is their digestion.

During a vacation-course on ants which I once gave at Salzburg, I succeeded in proving this point to about forty people, while we were out walking, by using a weak magnifying glass to watch some large aphids which certain *Myrmica rubra* were cultivating on a low oak-branch. As I passed the glass to each person, I requested him to place his left hand in front of his mouth to prevent his breath from frightening the little creatures, and thus all my company were able to obtain a good view of the ants, as they carried off and swallowed the drops which fell from the anus of the aphids. Huber has shown that *M. rubra* carries the aphid's little drop to its mouth with its antennal club before swallowing it.

Huber also demonstrated the cultivation of coccids (*Kermes*) by ants. I will now let him tell the story in connection with *Lasius flavus:*

". . . I placed them and their aphids in a box with a glass cover, leaving in the earth with which I provided them the roots of a few plants whose branches spread outside the the box. From time to time I watered the formicary, and by this means the plants, aphids and ants found abundant food in this apparatus. The ants made no attempt to escape. They seemed to be quite happy and contented, and tended their larvæ and females with the same affection as they would have shown in their own nests. They took great care of the aphids and never did them any harm, and the latter in their turn seemed to have no fear of the ants, allowing themselves to be transported from one place to another, and when they were put down, remained in the place chosen by their keepers. When the ants wished to remove them they began by caressing them with their antennæ, as though to induce them to abandon their roots, or to draw their probosces out of the cavities in which they were inserted. They then took hold of them gently above or below the gaster with their teeth, and bore them away with the same care which they would have bestowed on larvæ of their own species. I have seen the same ant pick up three large aphids in succession, bigger than herself, and carry them to a dark place. There was one which resisted her for a longer time than the others ; possibly it was unable to withdraw its proboscis, having fixed it too deep into the wood. I amused myself by following all the movements which the ant performed in order to make it relax its hold. She caressed it and seized hold of it in turn, until it yielded to her desires. However, ants do not always treat them so gently. When they fear that they may be stolen by ants of another species living near their own homes, or when the turf under which they are hidden is too suddenly uncovered, they snatch them up hastily and carry them to the bottom of their subterranean passages. I have seen the ants of two neighbouring nests quarrelling over their aphids. When those of one colony were able to break into the others' nests, they stole the aphids from their true owners, which in their turn often won them back ; for ants know the full value of the little animals, which seem to be designed for them by nature. This is their treasure. The wealth of a formicary consists in the number of its aphids or cattle, the equivalent of both cows and goats. No one would have guessed that ants were pastoral folk.

It seems to me probable that the yellow ants gather the aphids into their dwellings, since they are in the habit of carrying them unceasingly from place to place, and since it is they who derive all the advantages of this relationship, I am very much inclined to believe that the yellow ants, and all that are equally energetic, go in search of aphids along subterranean passages which they make among the roots, find them scattered about on the grass, and gather them into their nest. Otherwise, I cannot understand why there should be so many of them in these particular formicaries, for nowhere else are they so common. When I have found them under grass, they have generally been surrounded by yellow ants, which reached them by subterranean passages, and probably took them to their homes in the autumn. They

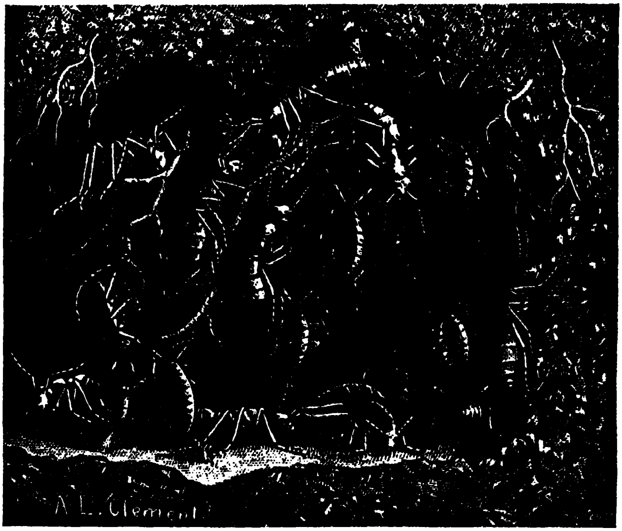

Fig. 90

often appropriated them in my presence, and retired with them by some obscure path, which proves that they dispose of them at their pleasure; it is chiefly in the cold season that they collect the largest numbers at the bottom of their nests. In summer, they are found more often at the foot of the plants near the formicary, because they suffer less from drought than those which grow on the nest itself. But here they are practically in the ants' home, for it extends infinitely farther inside the earth than outside."

Figure 90, after André, represents *L. flavus* with its aphids in a subterranean chamber.

I have said that ants cause their cattle to suck extra juice from the plant they are exploiting, and protect them at the same time. Bos has given an irrefutable proof of this by a comparative experiment. He grew some beans, infested with aphids, on a certain piece of ground, but prevented the ants from obtaining access to one particular patch. Here only a small number of aphids developed, and the crop was good. The beans to which the ants had access, on the other hand, were choked with aphids and yielded but a poor crop.

I have always insisted (*Fourmis de la Suisse*, second edition, 1920, p. 121 and elsewhere) on the harm which *Lasius flavus* does to our meadows by cultivating her aphids on the roots of the grasses, and etiolating them. But not long ago, Dr. Stäger (see Chapter III) put forward the view that this same *Lasius flavus* is very useful to the meadows in question, because it mines the ground as earth-worms do, and thus prevents the earth from piling up and hardening, acting as a ploughing process on a small scale, and at the same time supplying continual manure. This opinion seems to me worthy of every attention, and deserves to be verified by experiment.

It is chiefly the aphid-genus *Stomachis* which is reared by our *Lasius brunneus* on the trunks of poplars, willows, etc. They utilize the longitudinal rifts in these tree trunks to build tortuous covered roads out of inferior carton made from wood-rot, serving for the protection of the cattle. At the bottom of the rift, the *Stomachis* aphids suck the sap from the tree with their long probosces, reaching through the thin bark in those places which the ant-road does not cover. If you destroy one of these roads it is entertaining to watch the *L. brunneus* pulling with all their strength at the poor aphids, whose probosces, coming forth slowly from the bark, are stretched to such an extent that they are in danger of breaking. But when I did this, the *Lasius* would on no account abandon their precious cattle to an enemy, as they presumed me to be. Mordwilko declares that *Stomachis* is the usual aphid of *L. brunneus*, but this creature also carried some *Trama radicis* to one of its colonies which was in a state of famine. The *Lasius* ☿ soon began to palpate them with their antennæ, and to milk them.

Fig. 91

Fig. 91, after Mordwilko, shows this same *Trama radicis* as cultivated by our *Lasius umbratus* on the roots of *Artemisia*. *A* shows an adult *Trama* sucking, with its back legs upraised; *B* a *L. umbratus* palpating one of the aphids with her antennæ; *C* an ant swallowing the drop of honey-dew oozing from the anus of the *Trama; D* and *E* two *Lasius* transporting aphids between their mandibles; and finally *F*

Fig. 92

a *Tramà* carrying a droplet which hangs in the hairs surrounding its anus. Below on the left are some young *Trama* (larvæ).

Our *Lasius niger*, in particular, is in the habit of constructing extensions of her buildings round the stems of the plants surmounting her nest, covered roads or succursals.

These extensions reach a sufficient height to place the aphids under safe cover. Figure 92 is a faithful representation of such a structure, built around a celery-stem in my garden at Yvorne. It was drawn for me by Heinrich. But when the aphids are too far from the nest to be covered in by simple gallery-extensions or covered paths, certain ants build them special sheds of earth or carton. I have sometimes seen this done—for instance by some *Myrmica scabrinodis*, which built an earth shed a centimètre and a half long, along an oak

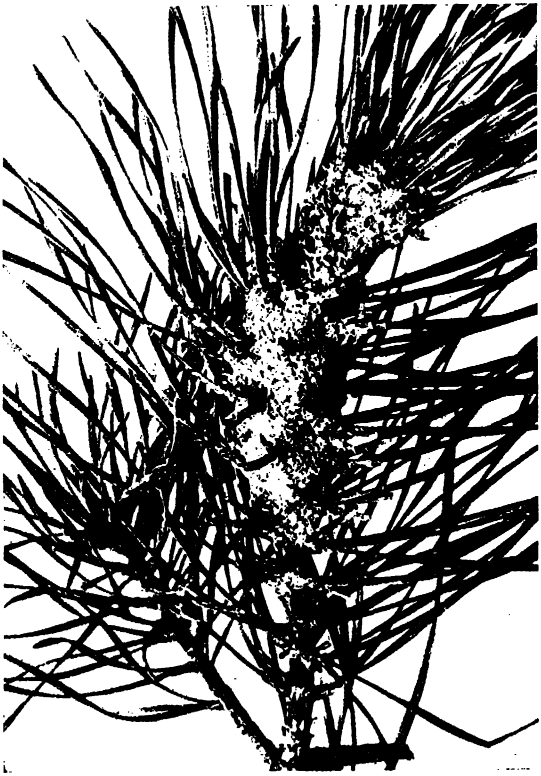

Fig. 93

INSTITUT POLYGRAPHIQUE S.A.ZURICH

E. W. Heinrich del. et col.

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a. *Calomyrmex splendidus* var. *viridiventris* ☿. Australia. 8·2 mm.

b. *Camponotus* (*Myrmepomis*) *sericeriventris* r. *rex* ☿. Central America. 13 mm.

c. *Camponotus* (*Myrmepomis*) *fulvopilosus* r. *detritus* ☿. Tropical South Africa. 12 mm.

bough entirely isolated from their nest. A very small hole, 1-1½ millimetres across, supplied the only passage for the ants, which were obliged to carry damp earth to the right spot on the little oak in order to build the coccids their cage or byre.

Fig. 93, after Wheeler, represents a similar but larger coccid-tent, built of carton by *Cremastogaster pilosa* of the United States, around a twig of pitch-pine, in order to protect their coccids in the same way.

The aphids and coccids require all this protection on account of the number of enemies which feed on them, and which are consequently friends to us humans. In the first place, there are the lady-bird beetles or *bètes à Bon Dieu* and their larvæ, which both live almost exclusively on the aphids; then the larvæ of a fly called *Syrphus*, and a lacewing, *Chrysopa*, which destroy quantities of them, and many more, such as spiders, earwigs, etc. When immured by the ants they are absolutely secure from all these murderers.

But many species of aphids do not attract ants, for example, those which live on roses. These have other means of defence; some secrete a milky substance all round them, others enclose themselves in galls, etc. Büsgen and Mordwilko have explained the true purpose of the two abdominal tubes which in several species of aphids, for example, the genus *Siphonophora*, secrete a viscous substance. Certain older authors imagined that the ants were attracted solely by the secretion of these two siphons, which they licked up. This error has been constantly repeated ever since. In reality, the aphid sprinkles the antennæ of its enemies with this secretion, which is at first liquid, but which at once becomes viscous in the air; in this way it often renders them helpless, as ants of the genera *Tapinoma*, *Azteca*, etc., render their own enemies helpless with the secretion of their anal glands, which we have mentioned before and shall have occasion to mention again.

On the other hand, many ants do not build any protection for their cattle—for example, *Camponotus* and the *Formica* of the *rufa* group, which cultivate woodland aphids known as *Lachnus*, found on pine-trees, and the oak-loving species known as *Dryobius*. In such cases they content themselves with making individual attacks with their mandibles and poison-glands upon every enemy that approaches.

Büsgen has watched an aphid supply 19 drops of honey-dew in 24 hours, and another as many as 48 in the same space of time.

The *coccids*, heavy creatures which cleave to their plant with scarcely a movement, are in certain respects still more productive for ants than the aphids, and are treated by them in the same fashion. The famous 'manna' of Biblical tradition, which fell from the sky of its own accord, is now known to be the excrement of a coccid, *Gossyparia mannifera*, which lives on the tamarisks. The Arabs of to-day still regard it as a delicious sweetmeat, and lick it from the leaves of the tamarisks, on which it is left by the coccids. In the amber epoch, and therefore long before Moses, the Israelites and the Arabs, ants already valued this manna. I myself once observed *Brachymyrmex Heeri* 'milking' the manna of two coccids, a *Lecanium* and a *Dactylopius*, in the orchid-house of the Botanical Gardens at Zürich.

In the United States, so Wheeler tells us, various *Cremastogaster*, *Camponotus*, *Myrmecocystus*, *Prenolepis*, *Lasius* and *Dolichoderus* show preference for the cultivation of particular coccids, especially the singular wax-covered species of *Orthezia* on the dry shrubs of the desert. *Azteca* cultivates numerous coccids in tropical America. According to Trimen, there is even a subterranean coccid cultivated by South African ants. In New Zealand, W. W. Smith saw an abundance of coccids (*Ripersia*, etc.), in the nests of the ant-genera *Huberia* and *Notomyrmex*, which are highly characteristic of this large Antarctic island. Thus we are clearly concerned with a world-wide phenomenon.

II CARE OF EGGS. But this is not all. Huber was the first to prove that the *Lasius flavus* ♀ herself tends and rears the brood of her aphids. Here again, I will leave the description in his own words:

"The aphids, which are viviparous during the summer, are oviparous in autumn. One day in November, being curious to know whether the yellow ants were beginning to bury themselves underground, I cautiously demolished their home, chamber by chamber. I had not advanced far in my excavations when I discovered an apartment containing a heap of little eggs, mostly the colour of ebony; they were surrounded by several ants, which seemed to be taking care of them, and which presently tried to carry them away. I first took possession of this apartment, its inhabitants, and the little treasure it contained: the ants did not abandon these eggs to make their escape easier; a more urgent instinct actuated them. They hastened to conceal the eggs under the little chamber I was holding in my hand, and when I got home I took them out to study them more attentively.

When examined under the lens, these eggs seemed to be of almost the same shape as those of the ants, but their colour was totally different. Most of them were black, but some were of a dull yellow. I found eggs in several nests, and obtained many varieties of shade. Not only were there black and yellow ones, but others which were brown, or a soft shade of red, or a bright and shiny red, or white; others again were of a less clearly-defined tint, straw-coloured, greyish, etc. I noticed that they were not of the same colour at both extremities.

The better to observe them, I had placed them in a box lid covered with glass. They were collected in a heap, like those of the ants themselves. Their keepers seemed to set great store by them; after visiting them, they carried away a certain number into the earth, but I was able to witness the care they bestowed on the others. These they approached, each slightly parting her pincers and inserting her tongue between two of the eggs, then stretching it and drawing it alternately across either egg, upon which I fancied I could see them depositing a liquid substance. They seemed to treat them in exactly the same way as those of their own species, palpating them with their antennæ, gathering them up and frequently carrying them to their mouths, but never leaving them for a single moment. They picked them up and put them back, and after examining them carefully, bore them away, handling them most tenderly, to the little earthen chamber I had placed near them. And yet these were not ants'-eggs. I was uncertain for a long time as to the origin of those I have just been discussing, and I discovered by chance that they contained little aphids, though I did not see any coming out of these same eggs, but only from some other and slightly larger ones which I found among some yellow ants of a particular species. On opening their nest I disclosed several apartments containing a large number of brown eggs. The ants were extremely concerned about them; they carried some of them away as quickly as possible to the bottom of the nest, and disputed their possession with me in a vigorous fashion which left no doubt as to their being strongly attached to them. In their interests and my own, I took the ants and their treasure and arranged them in a manner convenient for observation. These eggs were never abandoned, but received the same amount of care as the first. Next day I saw one of these eggs half-open, and out of it came a completely formed aphid, with a long proboscis. I recognized it as an oak-aphid. All the others were hatched a few days after, mostly in my presence. They at once began to pump the juice out of some of the branches of the tree I placed at their disposal, and the ants straightway discovered, close at hand, a recompense for the cares they had lavished upon them."

In 1907, Mordwilko confirmed all Huber's observations on *L. flavus*. He also found that *Lasius alieno-brunneus* bestows similar care upon its aphids' eggs, whereas *L. niger* and *L. umbratus* display an indifferent attitude towards them. Here, then, we have apparently a case of special adaptation on the part of two species of *Lasius* to the brood of their aphids, for hitherto nothing of a similar character has been observed in other ants.

Webster, in the United States, has also confirmed the fact that *Lasius americanus* cares for its aphids' eggs. He further proved that in the spring these *Lasius* transport their aphids to the roots of the corn, and place multitudes of them about the young, growing plants, so as to procure for them the freshest and tenderest roots. They even transport them to great distances, and in doing so take advantage of the rains after drought.

On the other hand, according to Mordwilko, *L. niger* in particular often cuts off the wings of the aphids, when they acquire them in their adult stages, so that they may be better able to swallow their drops of honey-dew.

III PSYLLIDS. These are little insects akin to the aphids but able to jump. Their relations with ants have been studied chiefly by Froggatt in Australia, where they are found for the most part on eucalyptus trees. In addition to an abundance of honey-dew, they produce solid excrement. But in many species the honey-dew is hardened into a shell-like form. This Australian manna is so abundant that the natives, and even the white children, take a delight in it. *Iridomyrmex detectus* competes with them and protects the psyllids. *I. nitidus* goes so far as to build thick covered paths round them, with a sheath of woody débris, on the trunks of the small eucalyptus trees—sometimes 4 or 5 feet above the ground.

IV MEMBRACIDS AND CERCOPIDS. The relations between ants and various species of these tree-hoppers (*Homoptera*) are similar to those just discussed. They have been observed by Belt in Nicaragua, by Baer in the Argentine, by Green in Ceylon, etc. Green observed *Centrotus* larvæ extending their long tails, which have jointed segments, to force out their drop of honey-dew every time an ant applied to them with her antennæ. Wheeler has made similar observations upon the Membracidæ of the United States, cultivated by various *Formica*. *F. integra* even makes them coverings of woody débris.

V FULGORIDS. Here I have myself been able to confirm the observations of Rouget, Puton, Delpino, etc., upon *Tettigometra* in Algeria. In 1894 I wrote as follows: *Tapinoma nigerrimum* climbs on to the shrubs and the tamarisk trunks; I was able to see how it cultivates the *Tettigometra* larvæ under the bark. These are very much like aphids, and are similarly cultivated and tended by the ants, as Lund pointed out in 1831, in connection with *Dolichoderus attelaboides*, etc. These little pale-grey larvæ can be seen clustering in the cavities of the bark, surrounded by ants which suck their sweet excrement and defend them. The larvæ which I saw were not covered with any such frothy liquid as the Cercopid larvæ form round their bodies by way of defence. Evidently the ants are adequate for this purpose. In a *T. nigerrimum* nest I discovered the adult insect, which was *T. decorata* Sign. I had already observed in Tunis in 1889 how *Tapinoma* transports *Tettigometra* larvæ to its nest. But we are in need of supplementary observations in order to study the intimate relations between the ants and these cattle, which are much more active than the aphids.

Silvestri afterwards made similar observations upon *Tettigometra impressifrons* and *costata*. They suck the underground roots in the nests of this same *Tapinoma nigerrimum*, which milks them. But according to Silvestri I was wrong on one point. He thinks that it is not excrement which the ants suck, but a secretion from cellular glands, four of which open on and under the prothorax and eight on and under the abdominal segments. But for that matter there is nothing to prove that what seems to us to be the excrement of aphids and coccids may not be, to a large extent at any rate, a secretion from the intestinal glands by metabolism (chemical transformation, assimilation and dissimilation). According to Torka, *Lasius niger* and *Formica cinerea* cultivate the *Tettigometra obliqua* larvæ which are found in great numbers about the roots of oats and rye.

Silvestri also found the larva of a lady-bird beetle, which, instead of eating *Tettigometra* larvæ as its fellows eat aphids, sucks their secretion and lives as a myrmecophile with *Tapinoma*.

VI LYCÆNIDÆ. Another curious kind of ant-cattle is the caterpillar of a beautiful little butterfly, with blue and other colours, belonging to the Lycænidæ. Excellent observations on the subject were made by Freyer as early as 1836, and more particularly by W. H. Edwards (1878) in the United States, de Nicéville (1888) in India, Thomann

(1901) in Grisons, and Viehmayer (1907 and 1910) in Germany. According to Viehmeyer, 65 species of such caterpillars are cultivated by various ants. De Nicéville and Thomann allowed me to share their discovery at the time. I give a summary of it after Thomann, who made his observations chiefly at Landquart in Switzerland.

Freyer had simply noticed that eight to ten ants were always to be found busied with some *Lycæna* caterpillars which were eating their leaves, and to which they never did any harm. Afterwards, in 1864, Ploetz mentioned cavalier-ants, riding horseback-fashion on the caterpillars, which went on browsing and were none the worse for being ridden.

Thomann has observed our *L. argus*, whose adult caterpillar is 1, 1·5 or 2 centimetres long, and browses in summer on the leaves and buds of a member of the *Leguminosæ*, genus *Oxytropis*, and those of a spiny bush of the genus *Hippophæ*. In the chrysalis state it only lives for two or three weeks. Thomann always found it in the company of *Serviformica cinerea* and *fusco-cinerea*.

At first he thought that the ants riding the larvæ were attacking them, but the constant symbiosis of the two insects soon undeceived him. He saw that this relationship was one of intimate friendship. Furthermore, the ants guided him henceforth in his search for caterpillars, even the smallest, which could scarcely be seen.

The ant climbs on to the caterpillar's back and directs its attention chiefly to the last segments of the abdomen, which it caresses persistently with its antennæ. Meanwhile the caterpillar nibbles away at its plant as though nothing were happening, and seems to find the occurrence quite natural, however many ants assail it. Thomann found not a single *Lycæna* caterpillar which was not accompanied by ants. As soon as a man places a finger near the caterpillars, the ants open their mandibles and defend them vigorously, so that they may even have to be forcibly removed from their backs. Edwards relates how a large ichneumon (winged parasite) approached a *Lycæna* caterpillar and surreptitiously tried to prick it with its ovipositor, in order to introduce its own egg into the skin of the unfortunate creature, which was being ridden by a watchful ant. The ant suddenly attacked the parasite with such violence that it fled without being able to carry out its cruel plan. But the ants did not always succeed, as Thomann proved. On the other hand, he saw a *F. cinerea* struggling to help a *Lycæna* caterpillar to climb back to its branch.

These caterpillars turn regularly into chrysalises in the chambers or galleries of their ant, and hang to the ceiling by their anal extremity and by a woven girdle. Thus they are secure against enemies. The ants guard and even protect the chrysalis until it is completely hardened, and also the caterpillar when it is casting its skin. Before the rains in India, according to Mrs. Willy, ants go in search of their adult Lycænid caterpillars with the purpose of transporting them in hundreds from the plants where they have been feeding to their subterranean chambers, where they put each one in the place which best favours its transformation into a chrysalis. At Landquart, Thomann only saw the ants accompanying the caterpillars which were about to turn into chrysalises.

De Nicéville, however, has given the following account of the occurrence in India: after six or seven days in the chrysalis stage, the butterfly is hatched; the effective help rendered by the ants during this operation enables it to come out and shed its skin, and it can then spread its wings normally, of its own accord, wait until they dry, and take to flight. When some accident occurs, which spoils everything and prevents the wings from developing, the ants may behave as did a *Pheidole* ♃, observed by Nicéville; she tried to help a *Lycæna* to climb back to the branch whence it had fallen, but as she had no success whatever, she finished by cutting off its shrivelled wings and then killing and quartering it. Thomann in Switzerland observed nothing of this kind. *L. argus* comes forth unaided from the chrysalis in its subterranean chamber, reaches the open air and climbs, still unaided, up some twig where it can spread its wings and quietly allow them to dry, quite near its ants, which refrain from doing any harm, but need do nothing more.

What does the Lycænid caterpillar do to make the ants treat it so well? They take no notice of the leaves which it gnaws, nor of its excrement. On one occasion only Thomann saw a *F. cinerea* take up, three times in succession, the excrement of a caterpillar which was gnawing an *Oxytropus* flower, in order to throw it away. This was a simple precaution of cleanliness. The ant's whole attention is directed, as we said before, to the middle of the third segment from the end on its caterpillar's back. What is the meaning of its repeated antennal caresses? From time to time it may be seen to press its mouth against this particular spot. There we may discover, even with the naked eye, a small transverse slit, absolutely identical with that drawn by W. H. Edwards for his account of the American species, and confirmed by de Nicéville with regard to the Indian species. In the adult caterpillar, this slit is ½—¾ millimetres long. It resembles a human mouth with its two lips. From time to time it opens, and out of the middle of it comes a tiny papilla, from which flows a little drop of transparent liquid.

This liquid is viscous, and ants dote upon it. The caterpillar never secretes it except when the ants beg for it or when the creature wishes to appease them. The same caterpillar can secrete it several times a minute or require a quarter of an hour's coaxing, according to circumstances. Observers assume that it is a sweet liquid, though they have never proved the fact by analysis. Thomann observed that the secretion came more frequently whenever the caterpillar felt itself to be in danger—for example, when it was placed on the observer's clothes, with its ant on its back. It seems as though it were instinctively trying to please the ant in order to obtain better protection. Thomann thinks it is evident that the honey thus secreted by *Lycæna* is one of the principal foods, sometimes *the* principal food of its ant.

In addition to this, on each side of the back of its last abdominal segment but one, *Lycæna* has a small protrusible tube or tentacle, with hairs at its extremity. The purpose of this tube has been the subject of much discussion. It cannot be used in defence as some have supposed, for the caterpillar thrusts it out only when in the presence of the ants, and not against its enemies. Thomann once enclosed ten *Lycæna* caterpillars with three ants in a steel box perforated with small holes. Other *F. cinerea* clustered round the box, making desperate efforts to get into it, and even trying to gnaw the steel. The moment the box was opened they rushed in and climbed on the backs of their caterpillars. When Thomann put some *Lycæna* caterpillars near some strange ants which had never had caterpillars, he noticed that at first the honey-dew was secreted abundantly, though the tubes were withdrawn. In this manner they succeeded speedily enough in changing their former enemies into good friends. The honey-dew then became rarer, but the caterpillars protruded their little tubes and the ants remained by their side. One large stranger-ant had handled a caterpillar somewhat roughly, but the *Lycæna* appeased her by secreting honey-dew to her. Suddenly the caterpillar gave up secreting, at the same time protruding its two tubes and beginning to move along. The ant then followed it, climbed on its back and faithlessly deserted the aphids which it had hitherto milked.

From these facts, and other similar ones, Thomann infers that the tubes in question project an odour which is agreeable to the ants and which attracts them, acting as a substitute for their honey-dew secretion.

There is another important point in this connection: the skin of *Lycæna* caterpillars is covered with little papillæ and large tactile hairs, some of which are furnished with nerves and have a certain analogy with the topochemical clubs illustrated in fig. 23 (Part I). Thomann noticed that when the *Lycæna* caterpillars are placed near strange ants of another species, or any *F. cinerea* which have no caterpillars —which amounts to the same thing—they immediately recognize them as such, close up their abdominal segments, make no movement, draw back their two little tubes and suddenly secrete a drop of honey-dew. As soon as an ant has discovered and swallowed this drop, the caterpillar begins the same performance over again, and thus changes the original hostility into friendship. Afterwards, however, it diminishes the ration and thrusts out its tubes, as we have seen. Thomann could never manage to make it secrete honey-dew by touching it with another strange object (a piece of wool, etc.). On the other hand, when brought near its own friendly ants, it no longer maintained a hostile or frightened attitude and returned to its former off-hand manner amid the swarming masses of old friends. Hence Thomann concludes that it distinguishes them from others, and thinks that it does so by means of a very fine sense of touch—to which I am inclined to add a sense of smell operating through the skin, though we cannot tell with any certainty.

In short, as Thomann worked over *Lycæna*, he came to the conclusion that the more it is examined the more it seems to resemble a myrmecophile caterpillar. Those which are otherwise form the exception rather than the rule, at any rate in the species with the slit which secretes honey-dew.

In 1910, Viehmeyer drew attention to an observation made by W. Schulze at Manila, in the Philippines, with some large *Catochrysops cnejus* chrysalises which were fiercely defended by *Camponotus* (*Myrmophyma*) *quadrisectus*, in whose nest they were found, between the roots of epiphytes. These Lycænid chrysalises have a secretory organ very similar to that of the *Lycæna argus* caterpillars.

Syndiaconic symbiosis seems to have become more or less indispensable to the caterpillars of many *Lycæna*, but it is certainly not so for any of their ants, which can obtain adequate substitutes. This is a final point which must not be omitted.

VII PSECADIA. The discovery in question was made by Thomann as a result of his studies with *Lycæna*. While observing ants, he saw some *Lasius niger*, some *Myrmica lævinodus*, some *Formica fusca* r. *glebaria* regularly accompanying the caterpillars of two small Lepidoptera, *Psecadia pusiella* and *decemgutella*, which are found in the Canton of Grisons on a plant called *Lithospermum officinale.* In Bohemia, a substitute for China tea is made with this aromatic plant.

The *Psecadia* caterpillar has no honey-dew gland. It moves about quickly and surrounds itself while young with a mesh of spun threads. Thomann was struck by the constancy with which the ants accompanied these caterpillars and defended them from all their enemies, and he therefore studied the matter more closely with a microscope, which enabled him to inform us that when the caterpillar nibbles at its plant and produces a scar there, the plant, which is very juicy, supplies to the injured part a liquid which the ants greedily lick up. It is when the pistil is eaten away that the ants concentrate upon a special effort. When the caterpillar nibbles methodically, the ants follow its mandibles as they move, to lick up the juice of the plant as it appears. In this case, therefore, the caterpillar's body is not directly exploited by the ant, which only uses it as a tool for triturating the plant in the right place. The caterpillar never enters the ants' nest, and the ants take no trouble with its chrysalis, nor do they ever lick either the mouth or the anus of the caterpillar itself; therefore they are especially greedy for the juice of the *Lithospermum*.

This, therefore, is a case of simple nutritive syndiacony of ants and caterpillars at the expense of the plant.

VIII FOOD OF ANTS IN GENERAL. The preceding account has shown that the sustenance of the ants is very complex and diverse. Some of them are carnivorous, others delight in sweet things, yet others in seeds or fungi. Most of them love variety in their diet. In connection with a new work on *Pseudomyrma* larvæ, Wheeler recapitulates the whole matter under ten headings, according to a method which I think will require some modification for the sake of clarity. We must not forget that ants themselves directly suck or rather lick the nectar found in the corolla of many flowers, not to mention the extra-floral nectaries which various plants possess.

1 DIRECT FOOD. (*a*) Prey torn in pieces, living or dead, chiefly by the primitive sub-family *Ponerinæ* and the *Dorylinæ*, but also by others ; (*b*) the nectar of flowers, etc., directly licked up; (*c*) Seeds gathered from plants (see Chapter V) and hoarded in granaries.

2 CATTLE. We have just described the various forms in

the present chapter. It may be divided into: (*a*) cattle sought and milked outside the nest; (*b*) cattle cultivated in the nest or its dependencies.

3 SPECIALIZED CULTURE OF FUNGI. For this I will refer the reader to Part V.

4 VARIOUS DÉBRIS. What is gathered up in the nest, refuse and kitchen rubbish such as excrement, fungi and scraps of food left under carton and in the chambers.

5 ALL KINDS OF DIRT. This is licked from larvæ, nymphs and companions or collected between the comb and brush of the spurs and tarsi, and accumulated in the buccal sac of adult ants, if not swallowed immediately. The microscope proves that these products are very complex and difficult to analyse.

6 In his work on the larvæ of *Pseudomyrma* and *Sima*, Wheeler had described and drawn a special large food-sac which these ants have behind their mouths, and which he named the *Trophothylax*. When examined under the microscope the ball of food contained in the Trophothylax proves to be filled, according to the species, with spores, pollen, insect débris, hairs, etc., similar to the contents of the buccal sac in adult ants, but mixed with fragments of insects which have been devoured. The Trophothylax is situated under another apparatus, regularly striated, which resembles the stridulatory organs, and which Wheeler has called the *Trophorhinium*. The purpose of these organs is problematic. They may be meant for a provisional cramming of the larvæ with prey and the contents of the buccal sac, or for *trophallaxis* (mutual exchange) between the larva and adult ant. Possibly the Trophorhinium may stridulate when the larva asks for something to eat, like a crying baby. As Wheeler says, we have not yet a microphone like that of Voltaire's Micromegas, to increase our hearing a

hundredfold and enable us to listen. We must therefore lay hypotheses aside and wait.

7 TROPHALLAXIS. Here I will refer my readers to No. 8 of our third chapter (*Paedalgus* and *Pachysima*), in which trophallaxis or mutual exchange of food between the larva and adult ant was explained.

8 PARASITES. According to Wheeler, the contents of the buccal sac proves that the ants occasionally devour some of their parasites, particularly their mites.

9 EGGS, LARVÆ, AND NYMPHS OF THEIR OWN BROOD. We have seen finally how ants may devour some of the eggs, larvæ, and nymphs of their own brood. Even the queen mothers, as we have seen, are guilty of such cannibalism towards their children. Guests and their larvæ may suffer the same fate on occasion. The above enumeration seems to me to leave nothing to be desired in the way of diversity with regard to the victuals savoured by the tongue and the ant's other organs of taste, in swallowing as well as in disgorging.

As for the food of the larvæ, I will continue to follow Wheeler, who has taken a very special interest in this subject.

1 The larvae of the *Ponerinæ* and some *Myrmicinæ* feed on prey, whole or in fragments, which the ☿ supply to them without cramming. As we have seen, they are sufficiently mobile and independent to eat alone.

2 The less independent larvæ of the *Dorylinæ* receive from their ☿ balls of food prepared beforehand from the prey.

3 The larvæ of the *Pseudomyrmini*, and perhaps those of the *Cryptocerini* and of some *Leptothorax*, are fed with the contents of the buccal sac of their ☿, with or without the addition of freshly-quartered prey. The *Pseudomyrmini* which inhabit acacia spines (see Plate VII, *H*, *B* [*a*, *b*], Part II) feed also on the 'Beltian bodies' produced by their acacias.

4 The larvæ of the granivorous *Myrmicinæ* are fed by their workers with fragments of seeds (see Part V).

5 The larvæ of the *Attini* (*Myrmicinæ*) like the adults, are fed on the products or 'turnip-cabbages' of the fungi cultivated by their ☿.

6 Lastly, the larvæ of some *Myrmicinæ*, *Dolichoderinæ* and *Formicinæ* are directly fed by their ☿, which disgorge to them the contents of their crops.

The larvæ, then, have also no lack of diversity in the matter of food; and with this I will conclude our fifth chapter.

Chapter VI

ANT-GARDENS

I must request my readers to look at figs. 94 and 95. The second, after Ule, represents two isolated ant-gardens,

Fig. 94

depicted at half their natural size and discovered at Bem Fim, Jurua, Brazil, in the district flooded by the River Amazon. Fig. *A* represents the earliest stages of a spherical garden, in which epiphyte seeds sown, according to Ule, by the ants, are just beginning to grow between the four ramifications of a tree-branch. Epiphytes, I may remind you, are plants which live as parasites on the branches of trees. Fig. *B* represents a little *Azteca* garden, surrounded by its earth, where epiphytes of the genus *Cordia* are growing. Ule tells us that these gardens look rather like sponges.

Fig. 95

Fig. 94 shows two ant-gardens made by *Azteca* amid the mazes of the tropical forest. The epiphytes on these are already large. In the ever-flooded forests above the banks of the Amazon, the epiphytes we find growing are of a somewhat specialized kind, and require a great deal of humus; they are represented by one member of the *Gesneriaceæ*, one of the *Bromeliaceæ*, one *Peperomia* and a few others. Here Ule frequently saw them collected on the balls of humus represented in our two figures. These balls are always inhabited by ants of the following species: (1) *Camponotus* (*Myrmothrix*) *femoratus*, (2) *Azteca Ulei*, (3) *Azteca olitrix*, (4) *Azteca Traili*, (5) *Cremastogaster limata*. Those of the last-mentioned species, which Bates had previously discovered on cutting open the swelling of an epiphyte with hanging aerial roots, seem to be rarer than the others.

It was in the flooded regions, where the trees are lower, better lighted, and interspersed with bushes—at Manaos, for example—that Ule found the best opportunity of studying all the stages of development in ant-gardens. These balls vary in size, some being as large as a nut and some as large as a human head. The *Gesneriaceæ* of the genus *Codonanthe*, which climbs by means of its thick-leaved branches, forms a particularly good starting-point, just where the branches of the tree begin to fork, for the formation of new ant-gardens, that is, new nests.

Ule writes as follows on the formation of ant-gardens:

"We thus see that certain ants sow flowering plants on bushes and on trees, and grow and tend them so that they can build their nests amongst them; they, therefore, build real hanging gardens which I have called 'ant-gardens.' The plants thus cultivated are related to humus epiphytes; these I have called 'ant-epiphytes.' I have confirmed the accuracy of this observation in various ways:

A It is impossible that these ant-gardens can be suddenly created each time the seeds of these epiphytes spring up. Moreover such a quantity of different seeds could not be brought at one time, whether by birds or other animals, or by the wind. Only the ants could be responsible. And besides, these ant-gardens are often built in places where other epiphytes are never found.

B The presence of special plants exclusively in the nests of these ants supports my view.

C The specific structure of ant epiphytes is such that they cannot grow without an artificial supply of soil.

D Finally, experimental attempts have shown me that the ants do in fact carry the seeds of their epiphytes to suitable spots."

Ule thus holds that ants carry humus and seeds to a convenient place which they have chosen. On several occasions he broke open the berries of 'ant-epiphytes' (Gesneriaceæ and Bromeliaceæ) and observed ants passing on to the branch. They then sucked the juice of the berry and afterwards took the stone and carried it to a well-protected part of their nest, the ant-garden.

On examining the structure of these nests and the cultivation of epiphytes by ants, Ule tells us, one is astonished to find how carefully they heap earth round the fragile roots of these plants during their earliest and tenderest stages. As the plant grows, the nest becomes larger and larger, and so does the slender masonry of its passages. The great majority of the numerous seeds which have germinated disappear, being choked by the others. Ule thinks that they were probably put there to give more solidity to the incipient nest and its subsequent building-work. The epiphytes which develop completely occupy between them the whole of the remaining space. If my readers compare fig. 95 with fig. 94 they will understand. As a rule, the Bromeliaceæ are more to the centre of the nest, the Gesneriaceæ farther out, and the Peperomia hang down from the exterior with their long branches. Ule sums up in this way:

"The ants sow and cultivate their special epiphytes which could not otherwise live. On the other hand these plants enable them to construct nests in the trees. These nests, thanks to the roots of the epiphytes, have the consistency required to resist the violent tropical rains as well as the scorching rays of the sun."

I may add that as ants can neither build nor dig out durable nests in flooded country, ant-gardens replace all structures of this kind, except the carton nests built by certain species. Even on dead trees, ant-gardens continue to thrive for a long time, acquiring a purplish colour, whereas other isolated epiphytes, not cultivated by ants, are doomed to die quickly. In view of all these facts I do not understand how Wheeler can still contend that "it is quite as probable that the seeds are sown by the wind."

Again, ant-gardens are not found exclusively in flooded countries, but also, though rarely, on the 'terra firma' of the Amazon forests in Brazil. As a rule they are built up against bushes or the forks of branches, sometimes even against plants or large leaves. A few of them, however, attain an enormous size and grow at the top of tall trees.

But this is not all. In 1910 I obtained from the Breslau Museum, in exchange for a woven nest, a hanging ant-garden measuring about 30 cm. in length by 25 in. breadth and 25 in. depth, gathered by Winkler at Hayvep in Borneo, together with *Camponotus* (*Myrmotarsus*) *irritabilis* var. *Winkleri*. One or two specimens of this variety, which was then new, were still to be seen in the nest. The garden was built round the bifurcations of five branches of the principal tree, the largest of which was 2½ cm. in diameter. All the epiphyte-branches were cut through by Winkler, and most of them (not all) proved to be hollow in the middle. They are easy to distinguish in that they can be moved in a piece along with the complete ant-garden, on the five branches of the tree, which constitute a fixed axis. The branches of the tree are not hollow. The fact that some epiphyte-branches are not hollow either proves that there are at least two different kinds.

The most remarkable thing about it all is the structure of the ant-gardens, which corresponds exactly to Ule's description of those found near the Amazon. It consists of a very fragile kind of carton, in its present dried-up state, looking just like dry humus, and containing within its walls all the fine ramifications of the epiphyte-roots. Thus we can see how and why the whole ant-garden moves in a piece round the five branches of the tree. The chambers and galleries of the nest are fairly spacious, while its walls of dry humus are somewhat thin. But its surface, which is sprinkled here and there with a little sawdust mixed with humus, is pierced by a number of small, round holes, too small to allow for the passage of the large *Myrmotarsus irritabilis*. This circumstance induces me to wonder whether *Myrmotarsus* was the real builder of the ant-garden, and whether it had been stolen by this ant, but we must wait a little longer before pronouncing judgment.

In § VI of the previous chapter, wherein we discussed the large Lycænid chrysalises, we saw that they were found by Viehmeyer *between the ephiphyte roots* in a nest of *Camponotus* (*Myrmophyma*) *quadrisectus* in the Philippine Islands. This is a large ant, but the chrysalises were large too. Can this also be an ant-garden? Viehmeyer raises the question, but out of it there arises another: can it be that ants use their gardens, sometimes or always, in order to rear cattle on the roots of epiphytes? Here is one more problem for the future to solve.

Finally, in his more recent work ("Parabiosis and the 'Ant-Garden,' etc.", *Ecology*, Vol. II, No. 2, April, 1921) Wheeler shows that he is still very sceptical as to Ule's statements regarding the sowing of epiphyte-seeds by ants in the ant-gardens which he observed. He demands, and rightly enough, that new and more extensive observations on this subject should be made.

Chapter VII

MUTUAL PARASITISM OF ANTS

There is a proverb, 'man is a wolf to man.' It is true alike of our individual and our collective life. And this proverb is also true with regard to ants—but only so far as the relations of different communities are concerned, as we shall see in Part IV. As for parasitism, which is very little better than wolfishness, its character is the same with regard to us and to them. In ants it is collective only.

In our second chapter we have already spoken of temporary parasitism of various kinds in certain ♀ which found colonies. This also occurs on behalf of the future community, though it often begins with a single individual. We need not concern ourselves any further with the matter here, where our sole task is to discuss cases in which a species of ants remains the definite parasite or guest of another species throughout the life of its formicary. We shall give a moment's consideration to twenty-three different genera, eighteen of which are exclusively and definitely collective parasites, and five of which include only one or two parasitic species. Apart from two species of the genus *Camponotus*, all these parasites belong to the sub-family *Myrmicinæ*. Some of them still have ☿, others have only ♀ and ♂ left, as the ☿ have become useless and have disappeared.

The present chapter has a direct connection with

Chapter IV of Part II, which deals with ant-guests, and also with Part IV, which is to follow. My readers will be able to trace this by means of countless transitions. For example, *Strongylognathus* and *Harpagoxenus* form a transition between slave-making and collective parasitism. Moreover, Wasmann's sub-division of the guests into *symphiles*, *synœketes* and *synechthrans* may also be applied to the collective parasitism of ant-species upon ant-species. In Part IV we shall discuss synechthrans under the heading of *Lestobiosis*. The present chapter is concerned with only one synœkete, the rest being symphiles. We will begin with the synœkete.

I FORMICOXENUS NITIDULUS. The earlier authors such as Forster, Nylander and Mayr, had drawn attention to this ant as a guest of *Formica rufa*, but had not described its habits. In No. 11, of Chapter VI, Part II, we have already quoted the curious double nests which *Formicox. nitidulus* builds in polycalic colonies in the large nests of *Formica rufa*, upon which it is a true synœketic guest. The ♂ of *F. nitidulus* is always apterous and very much like the worker (see Part I, Plate III, fig. *h* and *i* ☿), whereas the ♀ is winged.

In 1869, I had already observed *F. nitidulus* living with a *F. rufa* colony which was taken at Zürich and transported in a bag to Vaux. In a fragment of rotten wood in the *rufa* nest I found a chamber containing the brood of *F. nitidulus*, and this, with about thirty workers and the ♀, I placed in a flask with some *F. pratensis* from Vaux. Nearly all of them died, but not from fighting with the *pratensis* colony. I had established the *F. rufa* from Zürich in a meadow at Vaux. They behaved with indifference to the *F. nitidulus* which accosted them, and would strike them with their antennæ and even climb on to their backs. I could not find out how the *F. nitidulus* obtained food. I ascertained, however, that when the *F. rufa* emigrated to a new nest, more than 3 metres away from the first, their little guest contrived to follow them to their new dwelling. In 1886 I repeated the same observation in a more detailed fashion. The *Formicoxenus* emigrated with all their brood to the new *F. pratensis* nest. For the sake of comparison I put seven *Tetramorium cæspitum* among the *F. rufa;* in half an hour's time all of them were killed, while the *F. nitidulus* endured no ill-treatment of any kind.

We are indebted to Robert Stumper (1918) for the best study of *F. nitidulus*, and I propose to follow him here. In the first place, he demonstrated a complete series of transitional forms, from the small ☿ pure, without ocelli, by way of a larger ☿ possessed of ocelli, then various apterous ergatogynes which are more or less fertile, then apterous ergatogynes with a type of thorax similar to that of the ♀, and lastly by way of small ♀, with the rudiments of wings, to the normal winged ♀. Among the ♂, Stumper found in the same colony some individuals with well-developed ocelli, some with rudimentary ocelli and others entirely deprived of ocelli.

In the neighbourhood of Neuveville, at the foot of the Bernese Jura, Stumper studied twenty-two colonies, fifteen belonging to *F. pratensis* and seven to *F. rufa;* out of all these, nineteen contained *Formicoxenus nitidulus* nests. In a central *Formica* nest Stumper found almost as many *Formicoxenus* as *Formica* (thirteen—fourteen on an average). He, like myself, was always struck by the perpetual feverish restlessness of the little parasite. He saw some ♀ each carrying two ♂ at once on her back. The little formicaries were situated either in the cracks of the *Formica* nest-walls, or in empty snail-shells, or under the axils of dry leaves. The ♀ help the ☿ to carry the larvæ and nymphs!

Stumper's investigations upon the polycalic *Formicoxenus* colonies found in one *F. pratensis* nest are particularly interesting. These colonies occupy chiefly that portion of the *Formica* nest which is situated immediately below the surface. They consist of a large number of small nests, close to each other but separate. Stumper has drawn more than forty in a single section of a *Formica* nest. If that of a *Formica* is built on a rotten tree-trunk, small *Formicoxenus* nests may be seen mined in the wood, which they perforate with very minute chambers and galleries to contain the brood. Others, as we have seen, dwell in the cracks of the *Formica* nests or in empty snail shells, etc. The *Formicoxenus* of all these nests maintain friendly relations with one another, and form one formicary. Stumper confirms the fact that the *Formica* are entirely indifferent to them, whereas the *Formicoxenus* will never leave their *Formica*, without which they would apparently be unable to live. He has made no experiments which would enable him to state whether the *Formicoxenus* of different *Formica* colonies are enemies or friends. However, he placed about twenty of them in a colony of *Polyergus rufescens* with *F. glebaria* slaves and found that they were entirely ignored by these two species, and therefore supported by them.

Why do these ants live as parasites? It is certain that there is no mutual feeding-process for either adults or larvæ. But the peace-loving *Formicoxenus* is protected from all enemy ants by its powerful *Formica*. This, I think, is the reason for its synœketic symbiosis with this species.

The next problem is concerned with the food upon which our little parasite and her brood contrive to live, and the manner in which she obtains it. Stumper has made the following experiments on the subject:

a He once gave twenty-five *Formicoxenus* a crushed *F.*

pratensis larva, and on another occasion, some sugared syrup. They almost completely ignored the first, which eventually became covered with mould, and licked the second without much enthusiasm. I myself had made the same experiment in 1886, with a similar result.

b On August 28th, he let a large number of *Formicoxenus* fast in a steel box until September 5th. He then gave them another fresh *F. pratensis* larva which had been crushed. This time seventeen ☿ eagerly began to lick up the secretion of the larva with their tongues, making rhythmic movements with their abdomens meanwhile.

c On another occasion Stumper gave the same ants a piece of crushed grape and sugared water, which they sucked up with the same eagerness. Honey, on the other hand, was scarcely tasted and even entirely neglected after a few days.

d These three experiments show that *Formicoxenus* is omnivorous (carnivorous and frugivorous), but that it prefers liquid to viscous food. This fact induced Stumper to make some researches, immediately after five consecutive days of rain. He then proved in every case that *Formicoxenus*, like all abundantly-nourished ants, had a swollen abdomen: most of them had even whitish rings between their abdominal segments. Scarcely anything of this nature was apparent, however, in the *F. pratensis* which sheltered them. Now it is evident that as the rain trickles through an ant-nest made of various materials, it dissolves not only carbonates, phosphates, etc., but also a great deal of organic detritus in the humus. From this Stumper deduced that *Formicoxenus* feeds naturally, to a great extent at any rate, on the contents of the rain-water filtering through the upper layer of the *Formica* nest, and I agree with his explanation. He considers that it also accounts for the concentric arrangement of their polycalic colonies under the surface of the *Formica* nest. For my part, I have no doubt but that the rain-water which filters through the humus constitutes a fairly important item in the food of all ants, especially, as we said before, in that of the brood of the queen-mothers. But in the case of *Formicoxenus* this factor seems to play a specially important rôle.

Stumper has also ascertained that *Formicoxenus* infests the various nests of its *Formica* in any given district from a certain point outwards, that is, from one or two nests which he considers the central point or central nests of infection. These are the nests containing the most *Formicoxenus.*

The 'infection,' however, does not seem to injure the *Formica*, as this parasite is essentially harmless and peaceable in all respects. I have never seen it fighting with another ant. Nevertheless, in 1886 I saw some *Formicoxenus* ☿ transporting their companions upside down on their backs, in the manner of the *Myrmicinæ*, in the course of the migration mentioned above.

In the *Zeitschrift für wiss. Insekten-Biologie*, Vol. XVIII, 1923, Dr. Robert Stäger, of Bern, briefly describes his remarkable new observations of *Formicoxenus nitidulus*, where he corrects the grave errors of Stumper and myself. In the first place, this creature is less pacific than we thought. Stäger has seen it defend itself valiantly against a *Lasius niger* and even fasten on to its leg and bite it. Moreover, when threatened by the said *Lasius*, for example, it stops, raises its abdomen almost perpendicularly on the side from which danger is expected, turning its sting upwards at the same time. This manœuvre usually induces the enemy to beat a hasty retreat. But the most interesting point is this: when two of their hosts (*Formica pratensis*) were regurgitating honey-dew (as in the illustration on our cover) Stäger often saw *F. nitidulus* climb quickly on to the head of the regurgitator and secure the precious drop—so that the other *Formica* eventually withdrew. He even saw *F. nitidulus* climb on to the head of an isolated *F. pratensis* (that is to say, where there was no mutual regurgitation), and by caressing her mouth with its antennæ, go on begging until the *Formica* had (automatically) regurgitated a little honey-dew for its special benefit. Thus the so-called mystery of the nutrition of *Formicoxenus* is now clear.

But it follows from Stäger's discovery that these wicked little 'guests' are by no means indifferent synœketes (see Part II, p. 277), but hemi-symphiles, as Stäger calls them (see Part II, p. 271). We ought rather to compare them, as Stäger does, with *Leptothorax Emersoni*, which we are about to discuss under (3).

I am truly ashamed to have been so blind to these facts, both in 1869, and later in 1874, when I wrote in my *Fourmis de la Suisse* that I had seen *F. nitidulus* speaking to its *Formica rufa* with its antennæ and climbing on her back.

Two more species of *Formicoxenus* are known, *Ravouxi* (the guest of *Leptothorax unifasciatus*) and *corsicus*; but we know nothing of their habits.

2 SYMMYRMICA CHAMBERLINI. This little ant, a parasite of *Neomyrma mutica* of the United States, was discovered in Utah by Mr. F. V. Chamberlin, who, according to Wheeler, wrote about it as follows: "Nests of *N. mutica* are common in some localities near Salt Lake City . . . . the soil where they occur oftenest . . . . sometimes contains much 'alkali'. . . . . In several parts of a ten-acre field . . . . I found nests of this *Myrmica* containing the symbiotic species. Three of these compound colonies were present. . . . . I never succeeded in finding one of the compound nests elsewhere than in this particular field. My attention was drawn to the first compound nest by seeing two individuals of *Symmyrmica*

disappear into a burrow immediately following a *Myrmica* worker. Upon excavating, I found others of the symbiotic form, mostly collected in a chamber about 8 inches below the surface."

Wheeler failed to find any traces of *S. Chamberlini* in Colorado. The species must be rare or local. The still-unknown female is probably winged; the ☿ and ♂ are wingless, but the latter has on his thorax the rudiments of a scutellum, etc., which betray the fact that his ancestors were winged. Much smaller than *N. mutica*, *S. Chamberlini* has the general appearance and size, as well as the blunt, denticulate hairs of a *Leptothorax* (*Mychothorax*) *acervorum*. Incomplete as is our knowledge of the habits of this ant, everything points to an analogy with those of *Formicoxenus*.

3 LEPTOTHORAX EMERSONI AND L. GLACIALIS. The curious *L. Emersoni*, discovered by Wheeler in the mountains of New England, lives with *Myrmica brevinodis* var. *canadensis*. The *Myrmica* builds her nest in marsh-land or moss, and under tree trunks or stones. Near the surface of such a nest, *L. Emersoni* pierces a number of small cavities, communicating with those of *Myrmica*. It is a double nest, but separated from that of *Myrmica*, and the brood of each species is therefore separated from that of the other. *Leptothorax* runs freely about *Myrmica's* galleries, but will not suffer the other to intrude upon hers: whenever she tries to enter by breaking into her nest, *Leptothorax* leads her politely but persistently home again, and feverishly repairs the breach. The little parasite does not leave her nest to go foraging: she induces *Myrmica* to feed her in a manner that is as strange as it is interesting.

Both in the natural nests and the artificial apparatus, *Leptothorax* is seen to mount the back of *Myrmica* and lick her skin with feverish ardour, for two purposes: firstly to obtain oleaginous salivary secretion with which the *Myrmica* cover their companions when they clean one another, and secondly to beg for regurgitation of the contents of her crop. With this second aim in view, they caress the head and epistoma of the *Myrmica* which have just returned from milking their aphids. It is amusing to watch the consideration and affection with which the *Myrmica* treats these little creatures that are licking her. Sometimes she even breaks the walls of the *L. Emersoni* nest and tries to get in and obtain the stroking and pomading she loves so well. But *Leptothorax* does not appreciate this point of view. She seizes the *Myrmica* by the mandibles, antennæ or legs, and forcibly ejects her, as who should say: 'I like coming into your nest, licking you and making you regurgitate to me, but as for you, you have no business in my nest!' And thereupon *L. Emersoni* hastens to mend the breach, reconstruct the walls and make another little hole through which she alone can pass to and from the *Myrmica* nest. When the two species are placed together in a common apparatus, without any earth, *L. Emersoni* makes a pile of her brood, and surrounds it with a kind of living rampart, with the aid of sugar or other refuse, to obstruct the *Myrmica*. But intrusion may then be so frequent that the little parasite is obliged to yield and permit the mingling of the broods. The double nest is thereupon transformed into a mixed formicary.

So long as the two species remain together in a Lubbock nest, *Leptothorax* continues to make *Myrmica* feed her in the manner described above, and none of them approach the manger or feed independently. But when Wheeler isolated a colony of *L. Emersoni* in one apparatus, the hungry ☿ began to visit the manger and feed, somewhat clumsily at first, but in the same way as the other ants.

Wheeler thinks this indicative of the fact that the *symbiosis* of *Emersoni* with *Myrmica* must be comparatively recent from the point of view of phylogeny.

The natural nests of *Myrmica brevinodis* do not seem to suffer greatly on account of these comic little satellites, for even where they contain some hundreds of them, a large number of ♀ and ♂ of the *Myrmica* species are produced. Though a true parasite, *L. Emersoni* has lost none of its essential original instincts: building, feeding its young, and, if necessary, feeding itself. Miss Holliday and Wheeler have shown that many *L. Emersoni* ☿ have ocelli and a well-developed receptaculum seminis and ovaries (see fig. 18, Part I). These ☿ represent all the transition stages to the winged ♀ by way of numerous ergatogynes, which seem to have a tendency to replace ♀ and ☿ by future phylogeny.

Leptothorax glacialis, from the Rocky Mountains of Colorado, at elevations of 2,500 metres, is very near of kin to *Emersoni's* simple race which lives with the *alpina* variety of *M. brevinodis*. But this parasite bestows less licking on its *Myrmica* and withal obtains more frequent regurgitation from her. Wheeler has inferred, from his observations with apparatus, that this species is less independent than the typical *Emersoni*.

In these two *Leptothorax*, therefore, we see a transitional stage between the synœketic habits of *Formicoxenus* and the two conditions of symphilic symbiosis and colony-admixture. They are two first-rate humorists, equal in rank with the Javanese mosquito *Harpagomyia splendens*, observed by Jacobsen and discussed in Chapter IV. of Part II. The above data are taken from Wheeler.

4 PHACOTA. In 1862, Roger described this curious genus from a single ☿ of the species *Ph. Sicheli*, found in Andalusia, to which Emery, in 1895, added a second species,

Ph. Noualhieri. He found this ant in Algeria, in a nest of *Monomorium Salomonis* v. *subnitidum*, and inferred accordingly that the genus was parasitic. This is certainly very probable, but as neither of these two species has since been found again, the whole question still remains undecided—a field for future investigation.

5 MYRMOXENUS GORDIAGINI. In 1902 Ruzsky sent me an ant which he had discovered in the Kirghiz steppes of Russia, associated with *Leptothorax serviculus*, which is of practically the same size as itself. At my suggestion he baptized it *Myrmoxenus*. This little parasite has a ♂ and a ♀, both winged, and also a ☿. Ruzsky, however, made no observations upon its habits.

6 SIFOLINIA LAURÆ. A ♀ of this species, taken on the wing, was described by Emery in 1907. He found it to be akin to *Harpagoxenus*, and supposed it to be a parasite. This scant information is all we have on the subject.

7 MYRMICA MYRMICOXENA. A long time ago—about 1872—my brother-in-law, Edouard Bugnion, brought me from Anzeindaz, at the foot of the Swiss Diablerets, some 2,000 metres high, several winged ♀ and ♂ of a curious *Myrmica*. For some time I regarded them as simple aberrations of the two winged sexes of our *Myrmica lobicornis* from the Swiss Alps, owing to the fact that Bugnion had taken them in the very midst of a formicary, side by side with normal ☿, ♀ and ♂ forms of this species. The discovery at a much later date of a number of parasitic ants caused me to submit my old specimens to a new and careful examination. All their characters, the curved, non-elbowed and non-dentated form of the scape,as well as the shape of the nodes of the pedicel, the size, etc., proved to me that I had been mistaken, and that this was a parasitic species, not an aberration from *M. lobicornis*. Hence I baptized it *Myrmica*

myrmicoxena. Unfortunately, no one has since found *Myrmica myrmicoxena* again, but the ♀ and ♂ specimens in my collection, found in 1872, bear witness to its existence. In any case, the formicary in question was a mixed one.

8 STRONGYLOGNATHUS TESTACEUS. This ant will be represented by its ☿ in fig. 104 (Part IV), and we have already spoken of it in Part I in connection with phylogeny. But it deserves a place here, as it has become parasitic by its phylogeny, whereas the other known species of the genus, so far as we know, are still slave-makers, and their habits will be discussed in Part. IV.

This little parasitic ant was first discovered in Nassau in 1852 by Schenck, who described its habits. Von Hagens, myself and others authors then completed his studies. *S. testaceus* lives in a mixed formicary with *Tetramorium cæspitum* and its races and varieties, like all the other *Strongylognathus* known, in earth-nests whose domes are in no way distinguishable from those of other *Tetramorium* nests. This nest contains: (1) a host of *Tetramorium* ☿; (2) numbers of *S. testaceus* ♀ and ♂ in July and August; (3) certain rare reddish-coloured *S. testaceus* ☿—about one to every ten of the *Tetramorium;* (4) occasionally one or two winged *Tetramorium* ♀ or ♂; (5) the whole *S. testaceus* brood and many *T. cæspitum* larvæ or nymphs. These facts, which I frequently observed at Vaux and elsewhere in the last century, long remained an enigma for me, until Wasmann provided the solution in 1891, by discovering one of the large fertile *T. cæspitum* ♀ living on the most friendly terms with a little fertile *S. testaceus* ♀ in a large mixed colony in Bohemia. On paying me a visit at the lunatic asylum in Burghölzli, which I was directing, Wasmann allowed me to share his discovery and even showed me the two ♀ still living. In 1907, Wheeler and I were able to confirm

Wasmann's discovery by finding a fertile *T. cæspitum* ♀ along with ☿ and nymphs of *S. testaceus* in a mixed colony on the Petit Salève near Geneva. True, we could not find the fertile *S. testaceus* ♀, but the presence of the brood left the matter in no doubt.

Wasmann thinks that the little fertile *S. testaceus* collaborates with a fertile *T. cæspitum* ♀ to form a new colony. Wheeler considers it more probably that the fertile *S. testaceus* ♀ causes herself to be adopted by a pre-existing *T. cæspitum* colony whose ♀ afterwards lives conjointly with her. The observations of more recent authors seem to support Wasmann. In 1908, Mrazek easily induced a *T. cæspitum* colony-founder to adopt a fertile *S. testaceus* ♀. The fact that the nuptial flight of the two species takes place at exactly the same time also adds weight to the same argument. I will likewise refer the reader to the Chapter II above. Whatever may be the case, we must needs wonder why the *T. cæspitum* ☿ rear such large numbers of parasitic ♀ and ♂ and scarcely ever any of their own. I have always supposed, perhaps wrongly, that the reason for this is the smaller amount of effort required to feed and rear the little *S. testaceus* brood. But it is difficult, not to say impossible, to give experimental proof of this.

Again, we may wonder why the *S. testaceus* ☿ are so rare in the formicary, whereas their ♀ and ♂ are so numerous. The other *Strongylognathus* species all have a large number of ☿, but we often have some trouble in finding one or two among *S. testaceus.* Sometimes they are a little more numerous, but they are always swallowed up in a black sea of *Tetramorium.* To me it is evident, as I said in Part I, when speaking of phylogeny, that the worker of this species is gradually disappearing. In any case, she has ceased altogether to go out slave-raiding, and if she wished to go she would be absolutely incapable of doing so. In a preceding chapter we saw what the ♂ do, and also the little fertile queen-mothers, which are smaller than their husbands.

As for the ☿, they do nothing whatever. Nevertheless, when honey is given them they are capable of eating it without any assistance, which *Polyergus* is incapable of doing, but as a rule they obtain honey-dew from their *Tetramorium* by regurgitation, and do not leave their nest. In connection with phylogeny I have already mentioned the convincing experiment I formerly made at Vaux with a mixed *T.S.* colony which contained relatively more *S. testaceus* workers than usual. I allowed it to be attacked by the *Tetramorium* inhabitants of another simple and normal (natural) *T.N.* colony, contained in a bag with their brood. The *T.S.* came forth in a crowd, and the ☿ of their little parasite *S. testaceus* occasionally went out with them, as though by atavistic instinct, on perceiving an enemy. But the most curious thing of all was the way in which these little creatures seized hold of their *T.N.* enemies by the head and made violent efforts to pierce these heads with their sickle-shaped, toothless and pointed mandibles (fig. 104, Part IV), which were absolutely incapable of doing any such thing, and ran more risk of being broken themselves on the harder heads of the *T.N.* But they behaved valiantly and perished thus, clinging to their enemies' bodies, while their allies the *T.S.* were the sole conquerors of the *T.N.* However, it seemed to me that the tactics of *S. testaceus* sometimes tricked the *T.N.* into relinquishing the legs of their enemies they had clutched, as soon as they felt that they themselves were being seized by the head. After a time, nearly all the *S. testaceus* which attacked the *T.N.* individually were killed by their stings, while they could not in their turn kill a single enemy, and vainly bit the heads of the prisoners taken by the *T.S.* When the *T.S.* had defeated the *T.N.* they began to raid the larvæ and nymphs of the vanquished. The *S. testaceus* which were left alive tried to do the same. But here the humour of the situation became doubly strong. One of them would turn a nymph over and over, for instance, in all possible directions, to place it in a convenient position between the two hooks of her mandibles, but when she in a measure succeeded in doing it, her strength scarcely sufficed for such a burden: she clung to every blade of grass, fell down again and again, and turned her nymph over in some other way in order to take it up differently, altogether presenting a singular contrast to the rapid movements of the *T.S.*, which ran with their heads upraised, holding their burdens without clinging to anything. Several of these *S. testaceus* lost heart before they reached the nest, and laid down their burdens for the *T.S.* to carry.

So you see, friend reader, that the accessory services which the *S. testaceus* rendered to the *T.S.* were by no means proportionate to their enormous losses by death: without assistance, they would all have perished in a quarter of an hour. These facts make it perfectly clear that the manner in which *S. testaceus* caricature the slave-makers of the same genus, *S. Rehbinderi* and *alpinus*, is simply an instinctive reminiscence of the hereditary mneme of their ancestors, which is roused at the call to arms, giving the best possible proof of their phylogeny. A mixed colony of *S. testaceus* and *T. cæspitum*, which I observed in an apparatus, confirmed my impression that the *S. testaceus* ☿ are usually lazy, for the utmost they can do is to feed themselves. Still more curious is the above-described ecphory (awakening) of their ancestral slave-making and warlike instinct by the hereditary mneme. When left alone with their larvæ, the *S. testaceus* carry them about aimlessly and then abandon them without feeding them or digging chambers for them, whereas in the mixed colony it is the *Tetramorium* which do all the work, including the care of the brood, the feeding of all the adults, and the building.

9 ANERGATES ATRATULUS. This little parasitic ant was discovered and described by Schenck in 1852, but he did not understand its true nature. It was left for von Hagens to enlighten us as to its habits in 1867. He managed to watch the life of the same formicary for several years in the same place, that is, in the same nest—which is a very important fact. But these authors did not as yet realize that the genus in question was aberrant, absolutely different from all the others, and in 1874, before it was baptized, I named it *Anergates*, which means 'without a worker.' Von Hagens had, in fact, proved conclusively that this species was a parasite of *T. cæspitum* and had no worker of its own—a circumstance hitherto unknown among ants. I myself have confirmed the observations of von Hagens, and I as well as Adlerz, Wasmann, Janet, Wheeler and Crawley have made others. As I have already depicted this ant in detail in my *Fourmis de la Suisse* (second edition, 1920, La Chaux-de-Fonds) and as Wheeler and Escherich have done the same, I have not thought fit to represent once more this degenerate creature, with its one-jointed palpi, its apterous ♂, which looks more like a greyish louse with a slow and heavy walk than an ant, not to speak of its little winged ♀ with her elderly appearance and the hollow in the middle of her abdomen.

Apart from what we have just said, the following are the most important points. *A. atratulus* is found in every part of central and southern Europe, but its colonies are rare and very far apart. I have never found a number of them in the same district at the same time. It provides an absolute contrast to *Strongylognathus testaceus*, for neither von Hagens, nor myself, nor anyone else has ever been able to find in the mixed colonies of *Anergates* anything but the brood of the parasite, one of its fertile ♀, the sole mother of the formicary, its adult ♀ and ♂ and some adult *T. cæspitum* ☿. No one has found a trace of the brood or winged sexes of this latter species, which alone rears and feeds the rest, builds the nest and in short does all the work. What, therefore, is the origin of these adult *T. cæspitum* ☿, which take so much care of the little parasite, and more particularly how does it happen that such an excellent and conscientious observer as von Hagens can follow the life of one formicary for several years in the same place? This is the great question we have all tried to answer, without finding any complete answer.

The mother or fertile ♀ of the formicary is only, so to speak, a living ovary. Her abdomen is so extraordinarily swollen that it has very much the same appearance as that of the nurses represented in figs. 80, 81, and 82, but it is flatter from top to bottom, and less spherical, the extreme swelling being produced, not by the crop but by the ovaries alone. The abdominal segments no longer show except as small black islands on a dull white background. The ♀ herself, surrounded by a bodyguard of *T. cæspitum*, has become incapable of walking and even of setting foot to the ground. She stays in her place with her legs outstretched, letting herself be crammed, and, if necessary, carried about by her bodyguard. She has ceased to be anything but an egg-laying machine, and doubtless possesses a large receptacle for semen.

The ♂ is a curious animal. He is of a greyish-yellow colour and larger than the ♀, and though apterous he has a thorax built on somewhat the same model as that of the ordinary winged sexes, his nymph having the rudiments of wings, which disappear after hatching; this shows that his ancestors were winged. His large, stiff abdomen is curved backwards and furnished with enormous genital valvules. He frequently spreads his six legs laterally, instilling little rhythmic and apparently convulsive movements into all the joints at the same time, as lice do. The little black virgin ♀, which is much more lively than the ♂, often makes similar movements, especially when frightened.

Janet has proved that the mandibular glands of the ♂ are powerfully developed. Adlerz and Wasmann have further shown that the *Tetramorium* pay scarcely any attention to the little virgin ♀ (except to feed them), whereas they often carry the ♂ about and lick them assiduously. When an *Anergates* ♂ is licked in this fashion, he remains motionless, and folds himself up. It is evident that his skin or one of his glands secretes a liquid capable of attracting the desire of the *Tetramorium*.

When hatched, the *Anergates* ♂ and virgin ♀, which are incapable of obtaining food for themselves, are fed by their *T. cæspitum*. They may then be seen mating in crowds inside the nest or at its surface, always by adelphogamy or the union of brothers and sisters of the same mother, as we have seen above. I know of no ant union which is easier to observe, in either a natural nest, or an apparatus, or a plaster arena. The ♀ is not coy, and gives way without any ado. The ♂ climbs heavily on to her back and thrusts his sagittæ forcibly into her vagina. Copulation lasts for several minutes, longer than with other ants, and a ♀ and ♂ in the act of mating may often be put into alcohol without being detached from each other. Only after copulation, in these terrestrial nuptials, do the fertilized ♀ take wing and fly—whither . . . . ? This is the question we asked before, and the following experimental attempts have been made to answer it.

Adlerz, in Sweden, placed several virgin *Anergates* ♀ in a strange (unmixed) *Tetramorium* formicary. They were able to move freely and practically unperceived among the ☿. If the formicary contained a fertilized *Tetramorium* ♀, the result was very much the same. Adlerz also placed some *Anergates* larvæ, nymphs, virgin ♀ and ♂ in an artificial apparatus containing an ordinary normal *T. cæspitum* formicary. In every case the little parasite was amicably received. Wasmann made similar experiments with the same result, whereas certain *Strongylognathus testaceus* ♀ and ♂, which were placed among these same *Tetramorium*, were pitilessly slain.

But how does *T. cæspitum* adopt the parasite's fertilized ♀, and how and why does her own disappear? On June 7th, 1907, Wheeler paid me a visit at Chigny, and we called on my brother who lives hard by at Vaux. We all went out together to look for ants, and Wheeler discovered an *Anergates* formicary at the moment of copulation. Large numbers of fertile ♀ were preparing for flight by climbing plantain leaves. We secured the nest with the aid of a chisel. It contained the fertile *Anergates* female, with a large gaster, the brood and numbers of ♀ and ♂ in the act of mating. The *T. cæspitum* carried off the ♂, but neglected the ♀. We then took our *Anergates* to Chigny in a bag, and afterwards put various fertile ♀ near the openings of several natural *T. cæspitum* nests, which they immediately entered. When placed a long distance away, they began to search hither and thither until they found the opening of a *Tetramorium* nest, wherein to enter. The *T. cæspitum* ☿ never showed any sign of annoyance; they did no harm whatever to the little parasitic ♀, and even carried some of them to the nest, whereas they left several ♂ outside, though without injuring them. One *T. cæspitum* colony, however, proved to be less kindly; the *Tetramorium* ☿ seized *Anergates* ♀ and ♂ by the legs, wings and antennæ, carried them a long way off and left them. Some strange *Tetramorium* which Wheeler placed near the same formicary were at once killed. The *Anergates* ♀ behaved in the same way on each occasion, trying to get into the *Tetramorium* nest and killing some of the inhabitants when they were ill-treated.

The following year, I returned to Chigny to examine the *Tetramorium* formicaries which Wheeler and I had caused to be invaded by *Anergates* ♀; none of them had become mixed, and no trace of *Anergates* remained. But Crawley (*The Entomologist's Record*, Vol XXIV, No. 9, 1912) succeeded in getting a fertile *A. atratulus* ♀ adopted by a large *T. cæspitum* colony. As a result of the adoption, the *Tetramorium* ☿ killed all their own fertile ♀, as we shall find that *Monomorium Salomonis* does when it adopts *Wheeleriella*. Hence this experiment of Crawley's solved the problem of the foundation of *Anergates* colonies, hitherto so enigmatical. For further details I will refer the reader to Chapter II.

I have no wish to offer you conjectures as to the phylogeny of *Anergates;* apart from *Anergatides*, no other genus of the *Myrmicinæ* resembles them, except perhaps *Hagioxenus*, which like them is parasitic. All that we can say is that their extreme parasitism and obligatory adelphogamy represent a degeneration of the species and the prelude to its future disappearance. Adlerz observed two *Anergates atratulus* hermaphrodites, one of which was continually trying to mate with various ♀, whereas other normal ♂ strove, meanwhile, to mate with them!

10 ANERGATIDES KOHLI. This was the name by which Wasmann, in 1905, described a new ant, a parasite of

Pheidole megacephala r. *melancholica*, discovered at Stanleyville in the Congo by his colleague, the Jesuit Father Kohl. The two species live in mixed colonies, like those of *Anergates*. The *Anergatides* family had no workers but only winged ♀ and apterous ♂, which fasten themselves to the ♀. In the mixed formicaries the only *Pheidole* are ☿ and ♃, no trace remaining of their ♀ or brood. According to Wasmann the *Anergatides* ♂ seem to be slightly less degenerate than those of *Anergates*. I have received from Wasmann the two sexual forms of this curious ant, which differs greatly from *Anergates*, despite the similarity in their habits.

11 WHEELERIELLA. About the year 1905, Dr. Santschi sent me from Kairouan in Tunis, along with some *Monomorium Salomonis*, a unique and curious ant which at first seemed to be a parasite, as I told my colleagues. I described this creature, giving it the name of *Wheeleriella Santschii*. Santschi then began to seek for more; and during the broiling heat of August in Tunis he succeeded in finding some *Wheeleriella* ♀ and ♂, both winged, either outside the nest on cactus or inside mixed formicaries with their *Monomorium*. He then observed some fertilized ♀ on the ground running along on their long legs towards some *Monomorium Salomonis* nests. These nests are so common in those parts that one can hardly move a step without

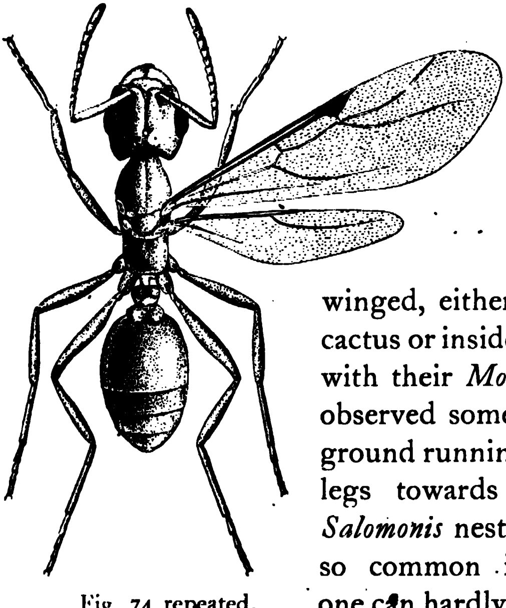

Fig. 74 repeated.

encountering them. I will ask my readers to look at fig. 74, which represents *W. Santschii.* The aim of the *Wheeleriella* in running is to approach as near as possible to the opening of a *M. Salomonis* nest before they are arrested by its inhabitants. The *M. Salomonis* ☿ even strive to arrest the *Wheeleriella* ♀ as she runs. When they manage to do so, she is generally already near the entrance. The *Monomorium* ☿ then take her by the legs and drag her into the nest, and the parasitic ♀ caresses them the whole time with her antennæ.

Being anxious to see this performance repeated near various *M. Salomonis* nests in the circumscribed region wherein the *Wheeleriella* were to be seen flying and settling, Santschi put a *M. Salomonis* formicary in a glass-covered apparatus and allowed a parasitic ♀ to enter, as she might enter a natural nest. He then set to work to observe. The *Wheeleriella* inside the apparatus continued to ingratiate herself with the *Monomorium* ☿, one after the other, by antennal caresses, until finally they suffered her to lie down unnoticed in a corner. She was not troubled by her rival or rivals—as there are often several fertile ♀ in one *M. Salomonis* colony, for excellent reasons. Hour by hour, the *Monomorium* became more and more friendly towards her and proportionately neglectful of their own mothers, which, within twenty-four hours, they were beginning to maltreat and then to mutilate and kill, to make way for the adoption of this insidious parasite. Santschi repeated this experiment several times, with the same result.

As soon as she is adopted, the *Wheeleriella* ♀ begins to lay, and her brood, fed and reared by the *Monomorium* ☿, is gradually and automatically substituted for their own. The *Wheeleriella* have no workers. The ♀ is 4-4·7 millimetres long, the ♂ 3·5-3·8; but both are absolutely dependent upon *M. Salomonis* for their food. The formicaries are never large, and it is evident that the *Monomorium* ☿, being unable to multiply further, must die out after a few years.

It is very instructive to compare the habits of *Wheeleriella* with those of *Anergates*. According to von Hagens, the *Anergates* formicaries may be perpetuated for several years, but we cannot be certain as to how far he is right. In any case, such a striking convergence of instincts between two such different genera is very remarkable.

Wheeleriella Wroughtoni. Mr. R. C. Wroughton once sent me from India a large number of *Monomorium Salomonis* r. *indicum* ☿, ♀ and ♂, all of which I had fastened on to some small cardboard triangles for my collection of duplicates. One day in the year 1910, whilst I was examining them, I noticed by chance one ♀ smaller than the others. I looked at her under the microscope, and she proved to belong to a new species of *Wheeleriella*, which I described under the name of *W. Wroughtoni*. On reading my description, the custodian of the British Museum sent me a whole bottle of this same *Monomorium*, likewise supplied by Wroughton, with a request that I should examine them. I discovered among them some new *W. Wroughtoni* ♀ and ♂, as I had done among my duplicates. It is clear that nothing is yet known as to the habits of this species, but the manner in which it was brought to our notice indicates that they are similar in character to those of *W. Santschii*, if not identical.

Wheeleriella adulatrix. In 1913 Santschi described under this name a new *Wheeleriella* ♀ which he discovered in Tunis, living with *Monomorium Salomonis* var. *subnitidum*, and whose habits seem to be very similar to those of *W. Santschii*.

12 EPIXENUS. In 1908, Emery described *Epixenus Andrei*, as the probable guest of *Monomorium venustum*,

judging from a ♀ taken between Jaffa and Jerusalem. He afterwards described *E. creticus* from a ♂ found in Crete. Some time after, I myself described *E. Biroi* from an ergatogyne ♀ found by M. Biro in a nest of *Monomorium creticum*, also in Crete. All the *Epixenus* ♀ are large ergatogynes, much larger than the ☿ of the ant upon which they live as parasites. Their ♂ is winged. The habits of *Epixenus* are unknown, but *E. Biroi* has been taken in a mixed colony along with *Monomorium creticum*. Emery thinks that these parasites no longer possess workers.

13 SYMPHEIDOLE ELECEBRA. This is a small parasitic ant discovered in 1903 in Colorado and New Mexico in the United States, by Schmitt and Wheeler. It lives in a mixed colony with *Pheidole ceres*. It has no worker, and the ♂ and ♀ are of the same size—less than 3 millimetres long. Despite a careful examination, Wheeler could find only the ☿ and ♃ of *Ph. ceres* in the formicary, and besides the adult *Sympheidole* a number of their pupæ. When Wheeler raised the stone covering the nest, the *Ph. ceres* seized the parasites and their pupæ and bore them away to the subterranean galleries. As there are generally from one to five de-alated ♀ in every uninfested *Ph. ceres* formicary, their absence from the mixed colonies infested by *Sympheidole* shows that they must have been eliminated in some way or other. As the *Ph. ceres* ♀ is twice as large as that of *Sympheidole*, Wheeler supposes that their own ♀ and ♃ commit the same matricide as *Monomorium Salomonis*, when polluted by *Wheeleriella*. This is possible, but it still remains to be proved. Here I have merely reproduced Wheeler's data.

14 EPIPHEIDOLE INQUILINA. In 1893 Emery received this little parasitic ant from Nebraska in the United States, and took her simply for an extreme microgyne (small female) of *Pheidole pilifera*. But in 1903 Wheeler

discovered near Colorado Springs three mixed colonies containing ♀ and ♂ of this little parasite and ☿ and ♃ of *Pheidole pilifera* r. *coloradensis*. No fertile ♀ of *Pheidole* was present. Hence we have here a parasitic species whose habits seem to be very similar to those of the species previously mentioned.

15 PARAPHEIDOLE OCULATA. In 1915 Emery described by this name a new species akin to *Pheidole*. It is a ♀ which Emery suspects of parasitism, though we lack proof of the matter.

16 PHEIDOLE INQUILINA AND SYMBIOTICA. Mr. Arnold, Director of the Rhodesia Museum, sent me from Bulawayo, along with some *Pheidole punctulata*, the ♃ and worker of another *Pheidole*, which he and I both suspect of being a parasite upon *Ph. punctulata* with which it was found. I have described it under the name of *Ph. inquilina*. But in this case also we must wait for proof. Wasmann has given the name of *Ph. symbiotica* to an ergatoid ♀ and a ♂ which was found with some *Ph. pallidula* ♃ and ☿, and which is very similar to that species. Wasmann regards as a parasite a certain little *Pheidole* ♃ which I consider to be a simple transition to its own ☿, but our best course is to be very prudent, lest in our haste we entangle still further a synonym which is already over complicated.

17 EPŒCUS PERGANDEI. More than twenty-seven years ago, Pergande discovered this little ant (afterwards described by Emery) near Washington in the U.S.A., living with the little *Monomorium minimum*, which is of a shiny-black colour all over. The parasite is of the same colour, and its ♀ and ♂ are winged. Pergande did not discover the ☿, nor has she been found since then. He declares that the *Epœcus* ♀ killed some *Monomorium* ♂ taken from the same formicary, when they were placed together in the same vial. Perhaps, as

Wheeler presumes, there has been some confusion here.

18 HAGIOXENUS SCHMITZI. In 1910, Father Schmitz sent me from Jerusalem a little winged ♀ of the *Myrmicinæ* which he took in a *Tapinoma erraticum* formicary. We know nothing more, but it is evidently a parasitic genus, and I have described it under the name of *Hagioxenus Schmitzi.*

19 SYNSOLENOPSIS BRUCHI. In the same way, Bruch sent me this species in 1918, taken in the nest of *Solenopsis tenuis* var. *Weiseri* in the Argentine. I regard it as a parasite, and have described it as such.

20 XENOMETRA MONILOCORNIS. This ant, described by Emery in 1917, was taken at St. Thomas from a nest of *Cardiocondyla Emeryi*, and is supposed to bear the same parasitic relation to this ant as those mentioned above bear to the genera with which they were found.

21 XENOHYBEMA MYSTES. In 1919 Santschi described under this name an ergatogyne ♀ related to *Epixenus*, but the ant which supports this supposed parasite is unknown.

The above twenty-one genera all belong to the subfamily of the *Myrmicinæ*. The following belong to *Camponotus.*

22 CAMPONOTUS UNIVERSITATIS. In 1890 I was present as a delegate of the University of Zürich at the celebration of the sixth centenary of the University of Montpelier. During a walk in the neighbourhood of this town I found several ant-nests, notably those of *Camponotus* (*Myrmoturba*) *æthiops*, a certain number of which I took; and afterwards I returned unsuspectingly to Zürich. Imagine my surprise when I examined my Montpelier ants, to find among the *C. æthiops* two smaller and totally different ☿, which I had evidently confused with the other species and taken in the same formicary. I was angry with myself, but it was too late. In describing this species I dedicated it to the University of

Montpelier. It is very peculiar in every way, and has stiff, truncated hairs like those of *Leptothorax*.

Several years later, while examining some duplicates of *C. æthiops*, which I myself had taken a long time before at Salève near Geneva, I was astonished to find among them, pinned by the same pin to a cardboard triangle, another specimen of the same *Camponotus universitatis*. Hence there can no longer by any doubt but that the species is a parasite upon *C. æthiops*, and lives with it in a mixed colony. We have no further information about it. I advise future ant hunters to examine the formicaries of *C. æthiops* and look for small ☿, which can be distinguished from this ant by the broadness of the thorax, among other things. The shiny-black colour is alike in both cases, and is apt to deceive.

23 CAMPONOTUS (MYRMOPSAMMA) SIMULANS. Schulze sent me a magnificent pale yellow variety of *Camponotus* (*Myrmopsamma*) *mystaceus*, distinguished by its remarkable macrochæte-psammophores, adapted to the desert. I gave the name of *exsanguis* to this variety, which was taken in the desert of south-west Africa. Between the mandibles of two large *Myrmopsamma mystaceus* v. *exsanguis* ☿ I found two small ☿ belonging to a little *Camponotus* of the same pale colour with the same beard of macrochætes, but of a different specific conformation, particularly as regards the presence of a little elbow at the base of the scape, which relates it to another species of *Myrmopsamma* which I have called *cuneiscapus*. My readers may judge for themselves as to whether I am over rash in deducing from my discovery that this little mimic is probably a parasite upon the large *mystaceus* v. *exsanguis*.

I might add to this already over-lengthy list two other cases depicted in our coloured Plate IV, *h* and *f*, Part II, as remarkable imitations of the form and colour of two other ants. I do not think this is a case of parasitism, but I regard it simply as a form of imitation or mimicry intended to protect the weaker species by enabling it to associate indifferently with the stronger, an arrangement which will become familiar to us in the course of Part IV under the name *parabiosis*. Here I will content myself with mentioning the fact by way of comparison with the last two cases, Nos. 22 and 23.

Thus Part III comes to an end, and it, too, as I said at the beginning, forms a transition to the following Part, which will deal with a matter full of topical interest for modern man—ant wars. Our little friends, like ourselves, pass from war to peace by means of alliances and *parabiosis*.